ANGLIA RUSKIN UNIVERSITY

THE ECOLOGY OF RIBAUTODELPHAX IMITANS (RIBAUT.): A SELDOM RECORDED PLANTHOPPER IN THE UK

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A thesis in partial fulfilment of the
requirements of Anglia Ruskin University
for the degree of Doctor of Philosophy

Submitted: 13th JULY 2016

ANGLIA RUSKIN UNIVERSITY
ABSTRACT

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This study is primarily concerned with the ecology of *Ribautodelphax imitans* (Ribaut.), a seldom recorded, data deficient and rare species of planthopper (Delphacidae: Auchenorrhyncha: Hemiptera) in the UK. Although it dealt with the ecology of this one species, it explored its community, related species and how they respond to habitat, host plants, and each other.

Firstly this project looked at the community position of *R. imitans* over a single season, clarifying its numerical abundance related to other species in its community. The lifecycles of many species could be modelled over the year; delphacids and cicadellids were mostly synchronous within each family. Monitoring the site over the course of several years also highlighted co-abundance patterns with a related planthopper *Javesella pellucida* (Fab.), which opened up avenues for experiments and comparisons between this species and *R. imitans.*

Host plant associations of *R. imitans* were investigated, as were the associated host plant networks of the Auchenorrhyncha community. It was determined that *R. imitans* was monophagous on tall fescue *Schedonorus arundinaceus*, but the community was dominated by generalist species. It was determined that in this typical grass feeding Auchenorrhyncha community, plant diversity was not the main driver for species richness however it was probably a factor in its stability. As tall fescue was the dominant grass on the study site, Coe Fen, it was determined that structures associated with this grass, tussocks, were important in the Auchenorrhyncha community.

Tussocks were investigated using survey and experimental manipulation approaches. Firstly the role of tussocks in grassland appeared to ameliorate the negative effects of declining sward height outside of tussocks - as a result of cutting and grazing - as more insects were found in tussocks surrounded by shorter swards than long. Secondly, there were contrasting responses of different groups to different aspects of tussock structure, it was thought that delphacids prefer denser and more nutrient-rich areas, whereas cicadellids prefer more open and less nutrient-rich areas of sward. These may relate to both their nutritional physiology and their biomechanics. The strong fidelity towards tussocks of its host plant could increase conspecific heterosexual encounters of *R. imitans*, thus maintaining high local population size and natality.

Lastly, interactions between and within species were investigated in a series of lab-based experiments. No effect of conspecific or allospecific density could be attributed to a change in developmental rate. However, there was evidence of host plant shifting in the generalist *J. pellucida* caused by the presence *R. imitans.*

The combination of host plant specificity, habitat specificity and competitive dominance feed into a model that would explain how rare species, or low-density populations can persist. However without fully understanding the distributions of species, one cannot be fully certain of its real distribution and status. This thesis provides a clear understanding of aspects of the species' general ecology, thus helping advise on how to collect further national records of this species, unlocking the key to its true status.

Key words: Auchenorrhyncha, host plant ecology, Delphacidae, Hemiptera, community ecology, interspecific competition, phenology, insect plant interactions

ACKNOWLEDGEMENTS

The author would like to thank his supervisory team Alvin Helden, Peter Brown and Toby Carter, for their support and motivation. Phillip Pugh and Nancy Harrison are owed special thanks for their mentoring and support throughout the course of my studentship and graduate teaching assistantship at Anglia Ruskin University. Gratitude is also owed to the other members of the Animal and Environment Research Group, in particular Dawn Hawkins, and Franc Hughes for getting me through the stage gates necessary for this studentship.

I would also like to thank, Nathan White and Amber Hatch and volunteers for the Cambridgeshire Wildlife Trusts, for help with their fieldwork. Also Rodi MacKenzie deserves special mention for his help with this project in its early stages with field and lab assistance identifying insects. Pete Stroh of the Botanical Society of the British Isles, also provided invaluable help with plant identification.

Cambridge City Council, Guy Belcher and Vic Smith have provided all the permissions and support for this work, without them it could not have been possible.

John Dover and Alan Stewart are to be thanked for their comments on this work and giving up their time for my exam. Alan Stewart also provided the records from the Auchenorrhyncha recording scheme used in this thesis, which I am very grateful for.

Lastly, thanks to all my friends and family for putting up with me whilst I tackled this project.

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Chapter 1

An introduction to Auchenorrhyncha and *Ribautodelphax imitans* (Ribaut.)

1.1 Introduction

The Auchenorrhyncha (Hemiptera) is an insect taxon that often dominates grassland ecosystems (Waloff, 1979; Nickel & Hildebrandt, 2003; Helden & Dittrich, 2016). They have been recognised as important indicator species by some sources, especially in grassland and forest systems (Andrzejewska, 1962; Hollier *et al.*, 2005; Moir & Brennan, 2007), as the group responds quickly to changes in environmental factors and management (Sedlacek *et al.*, 1988; Dittrich & Helden, 2012; Helden *et al.*, 2010). They have important roles in ecosystem function, being important in the diet of many species, especially birds (Buchanan *et al.*, 2006; Dennis *et al.*, 2008), spiders (Sanders *et al.*,

2008) and amphibians (particularly frogs and toads) (Stojanova & Mollov, 2008; Mollov & Stojanova, 2010). In spite of this they are often forgotten, their importance understated and research focused elsewhere. Just like many other insects, with the exception of some species such as butterflies (New, 1997; Filz *et al.*, 2013; Dover *et al.*, 2015), Auchenorrhyncha suffer from being a group of low conservation priority. Funding is often filtered towards more species poor, but higher profile taxa (such as birds and charismatic megafauna) (Leather, 2009). This work focused on one particularly little known planthopper *Ribautodelphax imitans* in a Cambridgeshire meadow. Not much is known about this insect other than there are very few records of its occurrence in the UK and this project sought to understand more about its ecolology.

It is rare for a meadow to be managed specifically for its insect inhabitants (Littlewood, Pakeman & Pozsgai, 2012; Littlewood, Stewart & Woodcock, 2012). However, when a nationally protected invertebrate species is present, desire by the land owner or legal obligation may result in specifically implemented management practices to improve the site for that species. One example is, the Million Ponds Project with the pondweed leafhopper *Erotettix cyane* (Boheman 1845) (Denton, 2004), for which special pond excavation sites have been dug and managed accordingly for this single species. Kirby (1992 a,b) produced both a review of the scarce Hemiptera of Great Britain and a book on managing habitats for invertebrates, but overall literature on specific habitat management and conservation for invertebrate species is scarce compared to higher taxa, with some exceptions such as butterflies (New *et al.*, 1984; Samways *et al.*, 2010). *Ribautodelphax imitans* (figure 1.1.1) is a nationally scarce planthopper (Hemiptera: Delphacidae) and one of only a small number afforded any specific conservation status in the UK;

however no such management plans are in place for *R. imitans* owing in part to the lack of specialist knowledge of its general ecology. Initial guidelines for its conservation were proposed by Kirby (1992), although these are in need of updating.

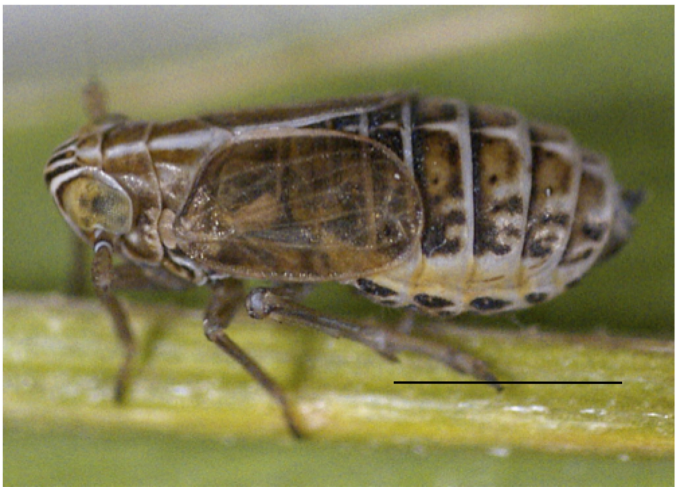

Figure 1.1.1: A female *R. imitans* found on Coe Fen, Cambridge 2012. The scale bar is 2mm (image Alvin Helden).

1.2 Auchenorrhyncha diversity in the UK and the status of *R. imitans*

The UK Auchenorrhyncha fauna is mainly composed of leafhoppers (Cicadellidae) [296 spp] and planthoppers (Delphacidae) [75 spp], although there are representatives from the Cercopidae [1 sp], Aphrophoridae [9 spp], Cixiidae [12 spp], Cicadidae [1 sp], Membracidae [2 spp], Issidae [2 spp] and Tettigometridae [1 sp] (Stewart and Bantock, 2015). The number of species on the UK list however is quite dynamic, with several new additions in recent years, since 2007 seven species have had been added to the UK fauna. These

include *Delphax crassicornis* 2009 (Skidmore, 2008), *Psammotettix helvolus* 2010 (Maczey and Masters, 2009), *Oncopsis appendiculata* 2010 (Ramsay, 2010), *Zygina nivea* 2011 (Bantock *et al.*, 2010), *Macropsis megerlei* 2011 (Bantock, 2011), *Dryodurgades antoniae* 2012 (Bantock, 2012) and *Pithyotettix abietinus* 2012 (Denton, 2012).

Historically Auchenorrhyncha have not been given the same level of protection as higher vertebrates (Myers et al., 2000; Biedermann et al., 2005) and other more charismatic insects such as the greater stag beetle *Lucanus cervus* (Coleoptera) (Thomaes *et al.*, 2008), and many butterflies (Lepidoptera) (New *et al.*, 1995; Brereton *et al.*, 2008). However there are a small number of Auchenorrhyncha considered conservation priorities, based on the now outdated Biodiversity Action Plan Framework (replaced within a Joint Nature Conservation Committee JNCC Framework)(JNCC, 2012). These species are: *Cicadetta montana* (Scopoli 1772), the UKs only true cicada (Cicadidae), restricted to the New Forest and now thought extinct in the UK; *Erotettix cyane* the pondweed leafhopper, restricted to just three sites in the UK; *Doratura impudica* Horvath 1897; *Euscelis venosus* (Kirschbaum 1868); *Eurysanoides douglasi* (Scott 1870); *Chlorita viridula* (Fallén 1806); and *Ribautodelphax imitans* (Ribaut 1953). All these species are in the UK red data book of endangered species (Kirby *et al.*, 1992*a*), however *R. imitans* is RDB-K, which indicates that its ecology and status are not known in enough detail to fully understand its rarity.

1.3 The general ecology of Auchenorrhyncha

Auchenorrhyncha as a group are obligate herbivores, both generalists and specialists, including a mixture of monophagous, polyphagous, and oligophagous

species (Holzinger *et al.*, 2003; Biedermann & Niedringhaus, 2009). The Delphacidae are one of the more speciose families of Auchenorrhyncha and arguably have the greatest proportion of monophagous species, certainly within the UK. Cicadellidae have a larger proportion of generalists, especially in grassland, although there are a still a large number of monophagous cicadellids particularly those that are found on trees and shrubs (BRC, 2016). Moreover, some species have life stage specific and seasonal dietary shifts (Prestidge & McNeill, 1983). Host plant relationships in much of the UK fauna are relatively understudied, apart from a small number of autecological studies (Waloff & Solomon, 1973; Waloff, 1980). Although, work in continental Europe has helped to elucidate some of these associations more recently (Nickel & Remane, 2002; Nickel, 2003), there is still a lot that is unknown, such as specific host plant associations, habitat preferences and phenology of UK species. As Auchenorrhyncha are recognised as an important contribution to UK biodiversity, functionally important ecological taxa, and indicator species further work on the ecology of individual species would be welcomed in the UK particularly as Stewart (2002) claims that in order for any species to be valued as an indicator its ecology must first be understood, and therefore their quality as indicators tested.

Lifecycles

Life cycles of planthoppers and leafhoppers differ greatly between species (Waloff, 1979; Nickel & Remane, 2002). They have varied overwintering strategies, as eggs, nymphs or adults depending upon the species (Masters *et al.*, 1998). Moreover, some species can have just one generation per year, whereas others have multiple generations per year (Andrzejewska, 1965; Prestidge & McNeill, 1983; Nickel & Remane, 2002). Some smaller typhlo-

cybine leafhoppers may have up to four generations in a year (Pers. Obs.). The UKs largest leafhopper, *Ledra aurita*, may take multiple years to mature to adulthood in certain limits of its range (Nickel, 2003). This could be related to interactions between insects' physiology, host plant characteristics and climate (Prestidge, 1982*a*,*b*; Prestidge & McNeill, 1983).

Community interactions: parasites, predation and disease

Auchenorrhyncha are important in ecosystems for a number of reasons. They are vectors for plant viruses, which has lead to efforts to control them in some commercially important situations (Saxena & Khan, 1985; Ammar & Nault, 2002). The prevelance and transmission of these viruses is linked with climate change, as the ranges of both virus and vector shift (Yamamura & Yokozawa, 2002), therefore it is possible that their movement on a global and national scale can indicate climatic changes and potential food security issues (Schmidhuber & Tubiello, 2007). In non-commercial systems it is possible that as vectors, they have roles in shaping the actual plant community structure (Saxena & Khan, 1985), however as the densities of insects in wild plant communities is much lower than in commercial situations the risk to plant loss is lower (Tedeschi & Alma, 2006).

It is well known that Auchenorrhyncha are an important food source for other animals, particularly birds, in part because of their abundance (Buchanan *et al.*, 2006; Dennis *et al.*, 2008), and for various parasite species. They are host to a number of different parasite taxa, and some of these parasites may have economic value, as Strepsiptera (Figure 1.3.1), mermethid nematodes (Helden, 2008), and wasps of the Dryinidae (Waloff & Solomon, 1973) are known to include biological control agents. Although to take a more biocentric view, Stork and Lyal (1993) claimed that when one species

goes extinct so does a whole suite of other parasite species, and that these extinctions are at least as common as host extinctions. The magnitude of this effect was later revisited in a review by Dunn *et al.* (2009) who refered to it as the 'sixth mass coextinction'. In fact coextinctions may be quite common in nature and without detailed understanding of host relationships, many species may be lost because of a lack of understanding of general ecology, be this through not predicting a loss of a host plant in a particular habitat or even through loss of an animal host species (Dunn, 2005; Dunn *et al.*, 2009). Species loss is a particularly contentious topic at the moment because of suggestions to eradicate entire species, for example *Aedes* spp. in South America to control the spread of the Zika virus (Hennessey, 2016), without fully understanding the implications of the absolute removal of one species.

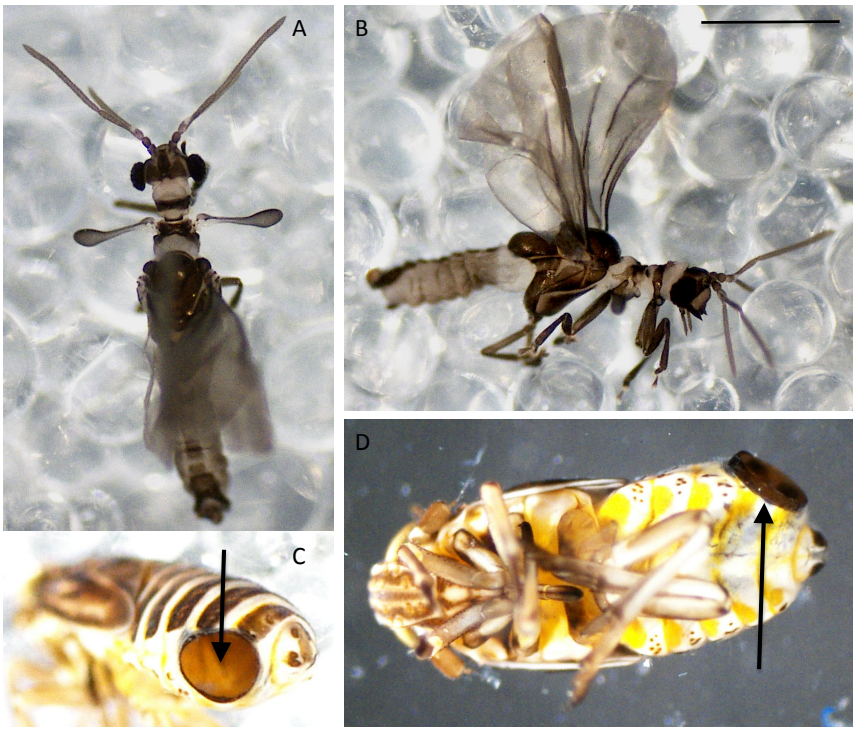

Figure 1.3.1: *Elenchus tenuicornis* (Strepsiptera) reared from a delphacid nymph A-B adult male view, C emergence hole and D remains of pupal cap. The scale bar in the top left Image is 1mm. Alex Dittrich.

1.3.1 Grassland host plant and structural habitat effects

Communities of Auchenorrhyncha can vary across different habitats, different latitudes and grassland types (Eyre *et al.*, 2001; Hollier *et al.*, 2005; Maczey, 2005; Waloff & Solomon, 1973; Waloff, 1980). The group also responds readily to changes in host plant quality and nitrogen content, with different levels dictating community composition (Prestidge, 1982*a*,*b*; Sedlacek *et al.*, 1988; Haddad *et al.*, 2000). However, the reasons for this are potentially confounded in that both host plant quality and plant structure are affected by

the addition of nutrients, particularly in agricultural systems (Prestidge & McNeill, 1983; Dittrich & Helden, 2012; Helden & Dittrich, 2016).

Plant structural heterogeneity is very important in grassland systems. It increases the number of available habitats, thus potentially more niches; which in turn benefits species richness. Where the grass is either heavily grazed, or intensive management techniques are employed such as cutting, areas of greater structural heterogeneity such as field margins (Bell *et al.*, 2002; Blake *et al.*, 2011*a*), tussocks (Cherrett, 1964; Luff, 1966; Bakker *et al.*, 1984; Maelfait & DeKeer, 1990; Bayram & Luff, 1993; Dennis *et al.*, 1998, 2001) and cattle sward islets (Helden *et al.*, 2010) are of greater relative value to insect biodiversity. However in any management regimen there are winners and losers, as not all species respond in the same way, some preferring different sward types to others (Littlewood *et al.,* 2012) .

Auchenorrhyncha can demonstrate positive responses to plant specie richness through management, with species compositions varying between habitats with extensive and intensive management practices (Hollier *et al.*, 2005; Littlewood, Pakeman & Pozsgai, 2012; Blake *et al.*, 2011*a*; Huusela-Veistola & Vasarainen, 2000; Maczey, 2005). In grassland, relationships between Auchenorrhyncha and plant species richness may be attributed to the microhabitat diversity provided by plants; rather than a large diversity of hosts supporting specialist consumers (Koricheva *et al.*, 2000; Hartley *et al.*, 2003). This is supported by the large proportion of species that are in fact polyphagous or oligophagous (Nickel, 2003). The belief that host plant relationships may be the most important driver for Auchenorrhyncha diversity in grasslands however, may be more complex than simple direct relationships between hosts and consumers (Kruess & Tscharntke, 2002*a*).

1.3.2 Intraspecific and interspecific interactions

Insects interact in different ways, directly with each other (conspectific interactions) (e.g. Horgan *et al.,* 2016), different species (heterospecific interactions) (e.g. Sun *et al.,* 2009) and indirectly by altering factors such as plant chemistry and defences (Denno *et al.*, 2000; Cao, Lü, Lou & Cheng, 2013). Competition is one of the most important interactions in ecology, because it drives niche differentiation, and therefore speciation (Dieckmann & Doebeli, 1999; Bürger *et al.*, 2006). However, in herbivorous communities there has been contention as to whether competition was an important driving force in community structure. It was thought that as plant resources were rarely limiting, so competition between herbivores must be rare (Shorrocks *et al.*, 1984); however this idea has since been strongly contested (Denno *et al.*, 1995; Kaplan & Denno, 2007). Competition is now thought to be very important in shaping communities of insect herbivores; particularly Auchenorrhyncha (McClure & Price, 1975; Stiling, 1980; Stewart, 1996; Ferrenberg & Denno, 2003).

The way that herbivorous insects such as Auchenorrhyncha interact is not clear cut. Interactions can be mediated by host plants (Poelman *et al.*, 2008) or differential predation (Denno *et al.*, 2003). Whereas resource limitation by one species, may affect the other; simply, leaving the another species disadvantaged (Kaplan & Denno, 2007).

Competition may drive the host plant choices that mediate community patterns, and be a major driving force in comunity structure. Although understudied in grassland systems, host plant preferences of generalists could be driven, to some extent, by the presence of specialists (Long *et al.*, 2007). It could be hypothesised that specialists should be better at utilising any one resource than the generalists that they share it with, otherwise what would be the ecological need for such host plant specificity?

1.4 Previous records of *R. imitans*

Prior to 1997 *R. imitans* was only recorded from Dorset and Devon (1959 and 1969). The species was then recorded in Dorset in 1997 and 2000, and East Sussex in 1998 (Stewart & Bantock, 2015). Following these discoveries there were some scattered observations of the species in Middlesex (2000), Essex (2006-2013), Northampton (2013), Lincolnshire (2013), Peterborough (2013) and most recently three sites in Cambridgeshire which include Coe Fen, Ouse Fen RSPB Reserve and Devil's Dyke (2011-2015) (figure 1.4.1, table 1.4.1; Stewart & Bantock 2016). However, records of this nature do need to be taken with some caution, as insect records are often patchy and suffer from under-recording, widespread species sometimes getting overlooked (Dunn, 2005) without the resolution of taxa such as mammals (Ceballos & Ehrlich, 2006). This aside, predictions of insect distributions can be made (Hassall, 2012); however they rarely come with the same resolution as information on actual distributions for other species, and they require a knowledge of the ecological conditions that the species requires. Potentially the most common planthopper in the UK is *Javesella pellucida* and even though its dominance in surveys illustrates this commonness (Stewart & Bantock, 2015), there is

still a large proportion of the UK without records of this species (Fig 1.4.1 right), in spite of high probability of its presence, attributed to its ecological generality and abundance in other studies (Quayum, 1968; Waloff, 1980). Therefore estimates of *R. imitans* distributions, of which in comparison there is very little ecological knowledge, need to be considered with caution. Evidence from other parts of Europe suggests that the species is rare throughout its range, however whether this is the case for this species in the UK remains to be seen (Nickel & Remane, 2002).

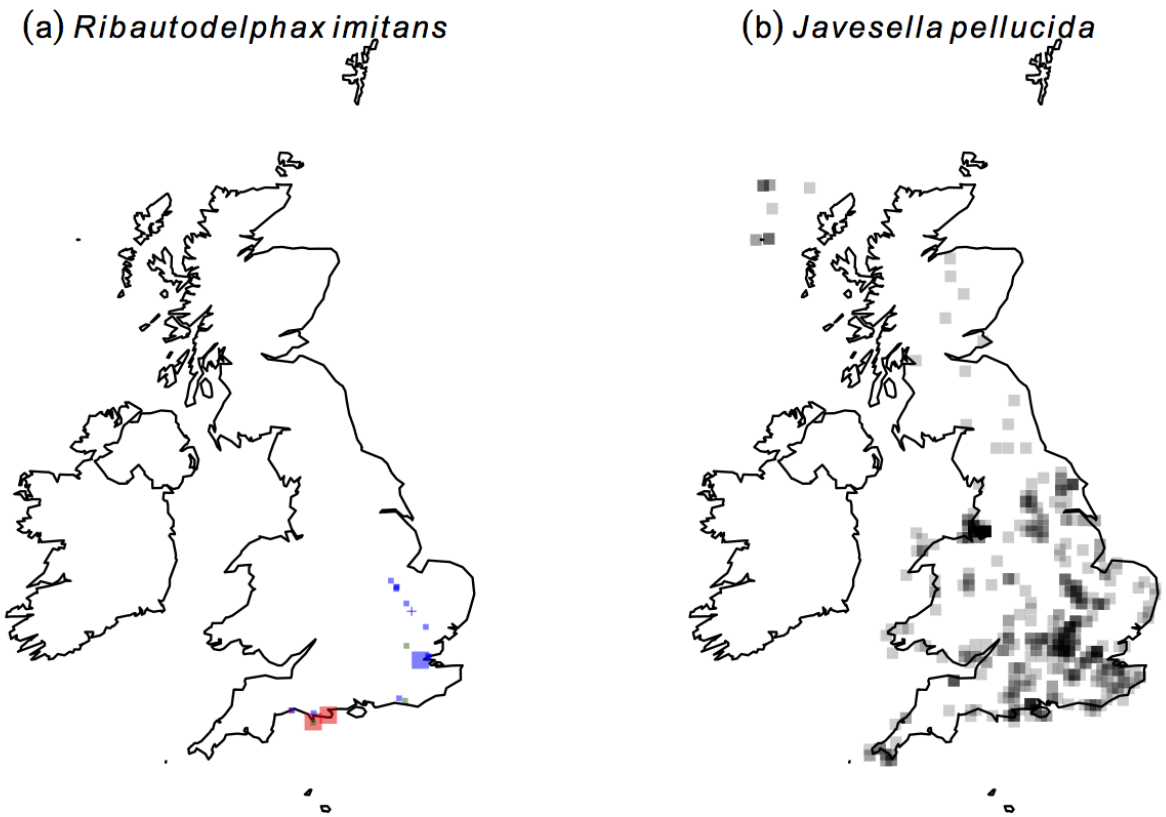

Figure 1.4.1: The distribution of *R. imitans* in the UK (a) compared to *J. pellucida* (b). The sizes of boxes represent the resolution of the data, be that 100m [smallest], 1km, 2km, or 10km [largest] squares, The squares are not to scale and merely representative of data resolution. Darker boxes represent incidents where there are overlapping records in close proximity. Colours on the *R. imitans* plot are indicative of the year that the data was collected: blue, 2000-present, green 1997-2000, and red pre. 1970s. The cross illustrates the location of Coe Fen. All data provided by the Auchenorrhyncha recording scheme (Stewart & Bantock, 2015)

Table 1.4.1: Observations of *R. imitans* in the UK from the Auchenorrhyncha recording scheme (Stewart & Bantock, 2015).

Grid reference	Latitude	Longitude	Location	Date	Site name / notes	Recorder
TL449576	52.197	0.119	Cambridge	2012-2015	Coe Fen	AJ Helden
TL351706	52.316	-1.942	Cambridge	Jul. 2014	Ouse Fen RSPB Reserve [single specimen]	AJ Helden
TQ260108	50.883	-0.210	Cambridge	Apr. 2013	Devils Dyke [single specimen]	AJ Helden
TQ767834	51.522	0.546	South Essex	Aug. 2013	Canvey Wick SSSI	PR Kirby
TL163947	52.538	-0.287	Peterborough	Jul. 2013	Orton Pit SSSI	PR Kirby
TL170977	52.565	-0.276	Northants	Aug. 2013	Thorpe Meadows	PR Kirby
TL171978	52.565	-0.274	Northants	Aug. 2013	Thorpe Meadows	PR Kirby
TF067082	52.661	-0.424	South Lincs	Aug. 2013	Casewick	PR Kirby
TQ779825	51.514	0.546	South Essex	2012	Canvey Island	T Bantock
SY292896	50.702	-3.004	South Devon	2011	The Plateau	CM Drake
TL710322	51.962	0.487	North Essex	2011		Essex Field Club
TQ6376	51.460	0.345	South Essex	2006	Tilbury	P Harvey
SY688845	50.659	-2.443	Dorset	2002	Bincombe	J Hunnisett
TQ372993	51.676	-1.714	Middlesex	2000	Rammey Marsh	P Harvey
TQ371070	50.846	-5.394	East Sussex	1998	Castle Hill NNR	AJA Stewart
SY677685	50.515	-2.457	Dorset	1997	Portland	MR Wilson
SY275895	50.701	-3.028	South Devon	1969	Axmouth-Lyme Regis NNR	MG Morris
SY6870	50.529	-2.453	Dorset	1959	Southwell	Hope Dept. Oxford
SY9681	50.629	-2.058	Dorset	1959	Corfe	BM(NH)

1.5 Rare species ecology and some of the problems with investigating rare species

Species can be considered rare based on their relative abundance in a community. They can also be highly specialised so only found in very narrow habitat ranges, or geographically they can be restricted leading to rarity (Cunningham & Lindenmayer, 2005). Many of the forms of rarity illustrated in figure 1.5.1, indicate that within communities many species are not numerically abundant, in fact most are rare; with those communities dominated with just a small number of abundant species (Ulrich *et al.*, 2010). This provides a compound problem to ecologists in that a lot of conservation effort is focused on rare species, and as ecological data is often dominated with zeros, it is hard to model the distributions of species that conservation efforts are geared towards. Local abundance and regional distributions are correlated therefore missing data or zeros make it difficult to model distributions (Tschartke & Dewenter 2002) .

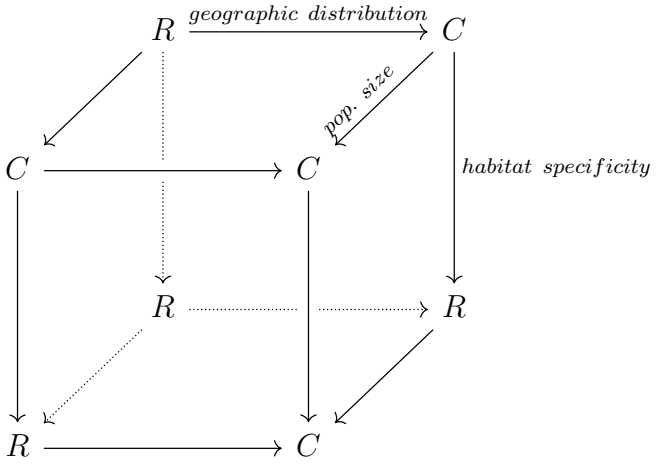

Figure 1.5.1: Conceptual cube diagram with three dimensions representing the three contributors to rarity; local population size, habitat specificity and geographic distribution. As there is increased pressure on one or more of these factors so does the likelihood of the organism being rare increase. The arrows indicate increasing one of these factors on an *X* - *Y* - *Z* axis. For example, in the forward top left corner we have common species (C), defined by their high population size and low habitat specificity, in spite of their narrow geographic distribution. In the bottom back right rare (R) species that in spite their wide geographic distribution, have small population size, and are very habitat specific.

Species rarity can be exacerbated by a number of factors. In the case of specialised species - particularly insects - rarity can come about because of host plant disappearance, scarcity or removal. Decreasing host plant range is related to rarity in a lot of cases (Hopkins et al., 2002) as is habitat fragmentation (reviewed in Tscharntke *et al.*, 2002). In some butterflies (Lepidoptera) however, specialists suffered as a result of habitat fragmentation, although the generalists increased in density because of the contribution of fragments to the overall landscape (Steffan-Dewenter & Tscharntke, 2000).

Some species' rarity may be characteristic rather than caused by any external effects, as some species may never be abundant throughout their range (Tscharntke *et al.*, 2002). Community structure could feed into this pattern of rarity as competition is thought to be a key factor contributing to rarity of some species (Ferrenberg & Denno, 2003; Kean & Miller, 2004). However, in the case of competition it is possible that exogenous effects upon the community, which may or may not be anthropogenic, could destabilise the structure leading to a competitive advantage of one species over the other (Rudgers & Clay, 2008; Sun *et al.*, 2009).

As Tscharntke *et al.* (2002) stated; rarity can be characteristic of a species. Understanding where the line is drawn between these two possibilities is important, especially where species conservation is concerned. Community effects, species autecology, and how communities and individuals respond to their environment are all key factors that need to be understood in detail, if any one species is to be conserved. *Ribautodelphax imitans*, the study species, is classed as a rare species and a UK RDB-K species, with insufficient data on its ecology, and little known of the factors underpinning its rarity. Without truly understanding a species ecology and how it responds to its environment, determining its conservation priority the reason for its rarity are hard to explain. *Ribautodelphax imitans* is a good example of this kind of paradoxical species; it has the status of rare but without a good understanding of why. Moreover, how can it be protected, if it indeed needs this protection, if little is known of its ecology?

1.5.1 Main aims and approach

This work aimed to elucidate more of the ecology of the planthopper *R. imitans* in a UK population; such as its host plant ecology, life history and

associated Auchenorrhyncha community. It is hoped this ecological work will feed into its conservation. If *R. imitans* is rare as a result of any potential anthropogenic effects, how can these be mitigated? In the broadest terms, the research undertaken was broken down into three question areas:

- How does *R. imitans* compare to the other species in its community in terms of its life cycles and abundance, is it part of a normal community structure?
- what environmental preferences does *R. imitans* have, including host plant and environmental factors?
- How does *R. imitans* interact with other species, and what are the ecological consequences of these interactions?

These questions were addressed through a series of lab and field based experiments. Host plant choices were examined in the field and in the lab; analysis of community structure in the field and how this insect community relates to the plant community. Lastly, intraspecific and interspecific interactions were investigated, looking at how the performance of *R. imitans* is affected by both conspecifics and allospecifics.

Chapter 2

General Methods

2.1 Field based experiments

2.1.1 Study site

Coe Fen (within OS Grid reference: TL4457; fig. 3.5.2 and 2.1.2) covers approximately 6.6 hectares of cattle-grazed flood meadow on the banks of River Cam, close to the city centre of Cambridge. The site is common land, managed by Cambridge City Council as a Local Nature Reserve (LNR). The site appears close to its current form on maps dated 1574 and is understood to have been cattle grazed grassland throughout its history much like it is today, although little is known of its exact grazing history (Anon, 2016*a*; Preston *et al.*, 2003).

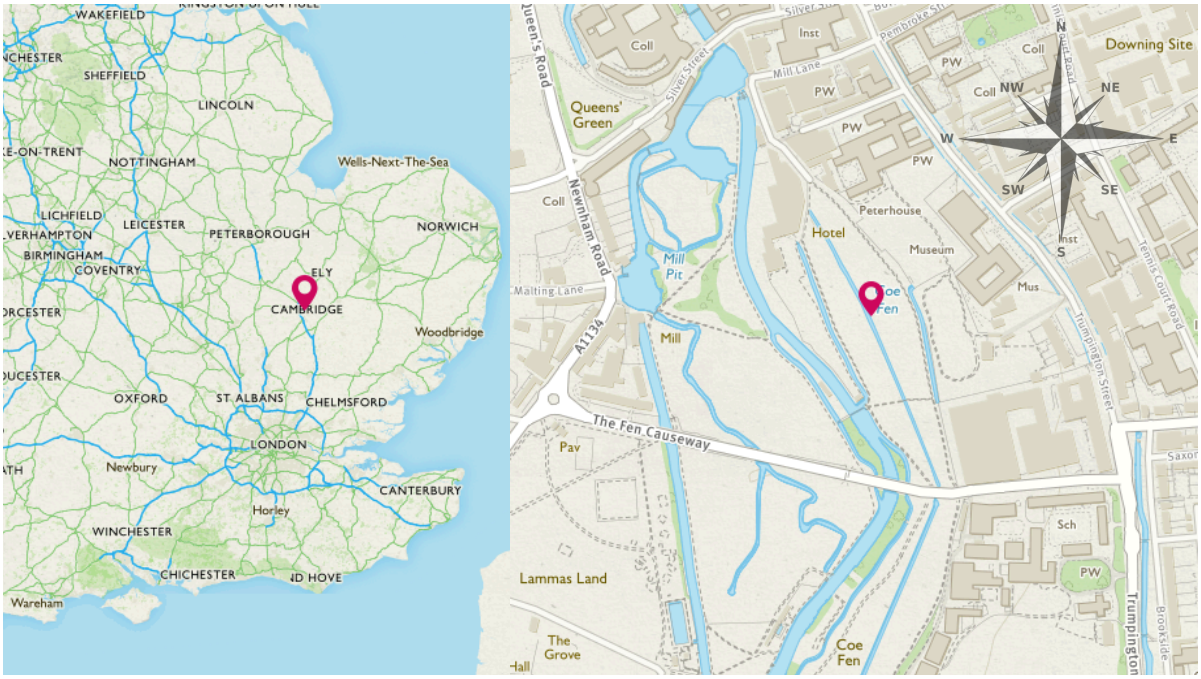

Figure 2.1.1: Map showing the location of Coe Fen in the UK (left) and in the its position in Cambridge city (right). The exact location is depicted with a downward facing arrow (adapted from Ordinance Survey).

In recognition of the site's ecological and recreational value, the City Council designated Coe Fen as a single LNR in July 2012. A Management plan covering 2012–2021 has subsequently been prepared in partnership with the Bedfordshire, Cambridgeshire and Northamptonshire Wildlife Trust (BCNWT) (Bedfordshire, Cambridgeshire, Peterborough and Northamptonshire Wildlife Trusts, 2012) . The fen forms part of a complex of natural habitats including the adjoining Sheeps Green County Wildlife Site (also included within the LNR designation), the River Cam County Wildlife Site, the riverside wet woodland known as Paradise LNR, and the Cambridge Botanic Gardens County Wildlife Site, as well as the international renowned College

Backs (predominantly formal riverside grounds) (Anon, 2016*a*; Preston *et al.*, 2003) (figure 2.1.1).

2.1.2 Monitoring of the site

The Auchenorrhyncha community on Coe Fen was sampled in 2011 at two-week intervals for a period of seven months from April to October. This enabled me to investigate relative population sizes of the different species in the community, and most importantly to evaluate the status of *R. imitans* (Chapter 3). For monitoring arthropod abundance and collecting sward height data data (see further chapters) the site was divided up into ten notional sections, which were based on their roughly equal size and their ease of locating based on fixed geographical markers (for example buildings and trees) (fig 2.1.2). Four random samples per section were selected prior to surveying with the locations determined in the field by pacing out the coordinates. All samples were collected used a Vortis Suction Sampler (Arnold 1994) with each sample emptied directly into a sweep net with a pooter used to extract all adult Hemiptera, which were later preserved in AGA (alcohol-glycerin-acetic acid) solution back in the laboratory (Gibb & Oseto 2006). Each sample consisted of 10 sixteen-second sucks on full power which were a meter apart from each other in a rough grid shape (Brook *et al.* 2008) , covering a total area of 0.2 m^2 (10 x 0.02 m^2).

Ten sward height measurements were taken with a pasture meter (Filip‘s Folding Plate Pasture Meter: http://jenquip.co.nz/products/filips-electronic-folding-plate-meter) /nociteAnonxx with each sample, the mean value was then calculated and used in analysis. All species were identified using (Le Quesne 1960, 1965, 1969, Le Quesne & Payne 1981, Biedermann & Niedringhaus 2009, Kunz *et al.,* 2011).

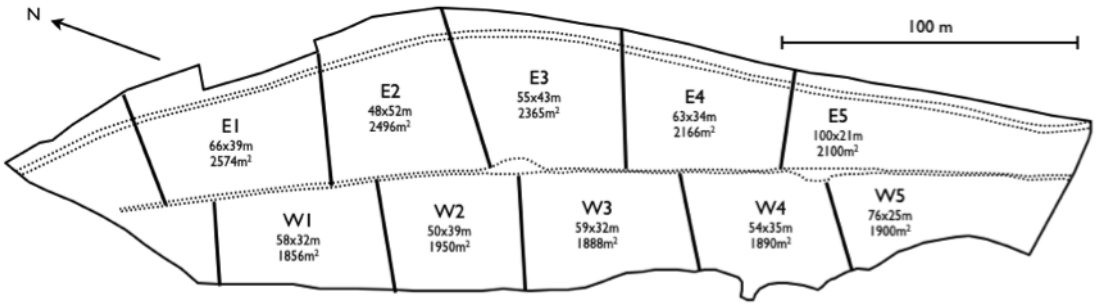

Figure 2.1.2: Map of Coe Fen, showing the ten notional sampling sections and their approximate dimensions. The dashed line in the middle denotes a small stream, and the dashed line at the top a tarmac foot path (Image courtesy of Alvin Helden).

2.2 Rearing of laboratory insects for experiments

To start the cultures, insect were collected from Coe Fen using suction sampler over June and July 2012, approximately 40 individuals of both *Ribautodelphax imitans* and *Javesella pellucida* were used with equal sex ratios for both species. Lab cultures were established and mass rearing occurred in controlled temperature conditions at 17°C ±1; 16 hours light, eight hours dark (L16:D8) under full spectrum artificial lighting (Osram^{TM} T8). Cages were simple 200 micron acrylic (www.ukcardcrafts.com), wrapped around to form a cylinder 13cm diameter affixed together with hot-melt glue (Loctite^{TM}: hot melt glue). Each cage had a small window 7x7cm in the bottom 6cm from the substrate over which was glued fine 5 micron netting (PlastOk^{TM}), in order for air to circulate. These cages were placed over the host grass in 15cm round plant pots (fig 2.2.1). Over the top of the cylinder was placed

5 micron netting (PlastOk^{TM}), which was held in place with elastic bands [these had to be replaced at regular intervals because of degradation]. The insides of the cylinders were cleaned with 70% ethanol to remove honeydew, a substrate for mould growth, approximately every six weeks. Also, to reduce humidity within rearing containers fine 4mm gravel was placed over the compost at the base of the cages, which appeared to inhibit both condensation and mould growth. Pots were placed in drip trays, and watered from underneath, approximately every two months. N 7.5% , PO_5 3%, K_2O 1.5%, Fe 0.125% liquid fertiliser was used to keep the plants in good condition, with plant colour used as a proxy for plant health.

Figure 2.2.1: Example of the cages used in insect rearing, and experiments.

2.3 Statistical methods

All statistical analysis were performed using R version 3.0.2 (R Development Core Team, 2013).

2.3.1 Chi Squared tests

For frequency tests Pearson's Chi–squared (χ^2) tests were carried out using Monte Carlo simulation; random re-sampling to calculate accurate p values.

2.3.2 t-tests

Students t-tests were used to compare means of normally distributed data. Normality was confirmed using Shapiro-Wilk tests (Shapiro & Wilk, 1965). Mean differences were presented with upper and lower 95% confidence intervals.

2.3.3 Generalised linear models

Generalised linear models (GLM) were used to model responses to multiple explanatory (independent) variables. GLMs are useful in that they are a generalisation of ordinary regression, but they allow for non normal error structures. This is done because it generalises the relationship between the response variable to the model via a link function (Nelder & Wedderburn, 1972). Both continuous and factor variables can be included in models that predict a given response, as well as interactions between these variables. After Nelder and Wedderburn (1972) The equation for the GLM is derived as:

$$E[Y] = \mu = g^{-}1[x\beta]$$

The outcome of GLM dependent variables are derived from an exponential distribution; $E[Y]$ is the expected value of Y, Where $x\beta$ is the linear predictor, from which the mean μ can be derived. Link functions $g^{-}1$ were typically either Poisson for count data, which have a log link:

$$x\beta = ln(\mu)$$

or binary outcomes which typically infer a binomial distribution and have a logit link between the parameter estimate and the mean of the distribution:

$$x\beta = ln(\frac{\mu}{1-\mu})$$

Conservative estimates of the 95% confidence intervals for each of the parameter estimates in the GLMs can be calculated by multiplying the standard error of the parameter values by the critical $z_{0.25}$ value for the normal distribution and adding or subtracting this from the outputted parameter value, for a normal distribution the value for $z_{0.25}$ is estimated at 1.96:

$$\theta \pm z_{0.25} \cdot \sigma_x$$

The $z_{0.25}$ value is derived:

$$z_{0.025} = \frac{1}{\sqrt{2}\pi} \int_{\approx.025}^{\infty} e^{x2}/2dx$$

2.3.4 R coding

Models in R were specified using the glm function from the core package. Model selection was always carried out using a stepwise deletion process, aided by the drop1 function, the lowest contributing factor dropped from the model, until the minimum adequate model was found (Manning, 2007). The 95% confidence intervals for all parameter values were calculated, using code

developed around the qnorm R function, which returns the probability for a normal distribution:

```
lower = coef(summary(model))[,1]
        qnorm(.025)*coef(summary(model))[,2]
upper = coef(summary(model))[,1]
        qnorm(.975)*coef(summary(model))[,2]
cbind(coef(summary(model)), lower, upper)
```

In addition, goodness of fit was calculated from the residual deviance and null deviance outputted from the model using the summary this is sometimes refered to as pseudoR^2 (Laitila, 1993):

$$R^2 = 1 - \frac{residual\ deviance}{null\ deviance}$$

Chapter 3

The local population status of *Ribautodelphax imitans*: community associations with other Auchenorrhyncha, phenology and life history

3.1 Introduction

Development and life cycles of Auchenorrhyncha vary between species and are strongly influenced by environmental conditions (Masters *et al.*, 1998). The two dominant grassland groups of Auchenorrhyncha, Cicadellidae and Delphacidae are largely asynchronous in the UK (Waloff, 1979, 1980) and continental Europe (Andrzejewska, 1965), however there are subtle differences between species within each group in their adult life cycles (Nickel & Remane, 2002) and instar durations (Prestidge, 1982*b*).

In managed systems such as cut meadows understanding life cycles and phenology of species is important from a management perspective to minimise disruption to sensitive species and populations (Lafage & Petillon, 2014; Blake *et al.*, 2011*b*). Management can have differing effects on both host plants and the insects that are dependent upon them (Littlewood, Stewart & Woodcock, 2012; Branson *et al.*, 2006; Helden & Leather, 2004). Top down effects on plants, such as cutting and grazing to prevent succession, may reduce competitive dominance by one or a few species. As one species may simply out-compete the others leading species poor plant communities (Hunter & Price, 1992; Siemann, 1998). Extensive management (such as low intensity grazing) in the long term has beneficial effects for the invertebrate community, illustrated by increased species richness, and abundance. These effects are linked to increases in sward height and structure with decreasing intensification (Kruess & Tscharntke, 1994; Dennis *et al.*, 1998). However, without appropriate management these short term improvements rarely persist and appropriate stewardship required to maintain this diversity; these include Agri-Environment Schemes (Dobbs & Pretty, 2004; Sutherland *et al.*, 2006) and local scale changes such as field margin managment (Blake *et al.*, 2011*a*).

Studying phenology and life-cycles of species also highlights how communities are composed. Understanding co-occurrence of species is important because it is the first step in highlighting possible competition. Competition is one of the main drivers of evolution (Hardin *et al.*, 1960) but until relatively recently it was a somewhat contentious subject within herbivorous insect communities because it was believed that competition was not an important driving force structuring insect herbivore communities (Shorrocks *et al.*, 1984; Jermy, 1985). A lack of belief in its importance led to a tempo-

rary dip in the study of interactions between herbivorous insects; however, the issue is now resurgent, and the importance of competition appreciated (Denno *et al.*, 1995; Stewart, 1996; Denno & Kaplan, 2007; Kaplan & Denno, 2007). As competition drives rarity in some species (Kean & Miller, 2004; Ferrenberg & Denno, 2003) and this thesis is concerned with the ecology of a rare species, it is important to understand which species are co-occurrent. Rarity of the study species, may not caused by one universal factor however, and competition is just one of these. Understanding whether rarity is driven by community effects is important because of the link between competition, and understanding community structure is the first step in elucidating these ecological conundrums.

This chapter highlights differences in the community position between *R. imitans* and related insects, comparing and contrasting life cycles and abundance patterns of the species through twice monthly monitoring. The site was also surveyed for Auchenorrhyncha twice yearly for a period of four years, and a series of lab based experiments designed to elucidate aspects of growth and development in *R. imitans*. Comparisons were also drawn with the delphacid *Javesella pellucida* on account of its national and local commonness, and its co occourance with *R. imitans* on the site. It was hypothesised that the lifecycle of *R. imitans* was comparable to those of other delphacidae, but dissimilar from those cicadellids found on Coe-Fen, as demonstrated in some earlier autecological work (e.g. Andrzejewska 1965). Likewise it was thought that the development of *R. imitans* may had some dissimilarities from other species, which could be related to its developmental ecology and potentially competition.

3.2 Aims

1. Assess the population status of *R. imitans* on Coe Fen.
2. Understand the life cycle of *R. imitans* and how this compares to other members of the Auchenorrhyncha community.
3. Quantify the community composition.
4. Work out whether there are any seasonal relationships between *R. imitans* and other species which vary year on year by monitoring of the site.
5. Quantify the development of *R. imitans* and *J. pellucida* and how these contrast using laboratory models, highlighting potential competition and coexistence strategies.

3.3 Methods

3.3.1 Field based methods

Samples of Hemiptera were collected on fifteen occasions between April and October 2011, at approximately two-week intervals (7 & 21 April; 5 & 20 May; 2, 14 & 30 June; 14 & 27 July; 15 & 24 August; 9 & 23 September; 3 & 18 October). Samples were taken from each of the ten plots on Coe Fen (see methods chapter).

3.3.2 Mapping the effort of Auchenorrhyncha recording in the UK

The number of records received per 10km square, were requested from the UK Auchenorrhyncha Recording Scheme (Stewart & Bantock, 2015) and sorted into the number of records per 10km square. In order to assess this visually, maps were produced showing the coverage of recording densities of less than 5, 10–50, 50–100, 100–200, 200–300, 300–400, 400–500, 500–1000 and more than 1000. The ranges were selected to illustrate the broad distributions in the numbers of records submitted per 10km square.

3.3.3 Development times of *R. imitans* and *J. pellucida* in the laboratory

Insect rearing conditions were identical to those in the general methods (Chapter 2); the temperature and lighting regimen analogous with the typical growing season these insects experience, and analagous with other laboratory studies on delphacid development (Raatikainen *et al.*, 1967; Quayum, 1968; Iwanaga *et al.*, 1985). Newly hatched, singly housed *R. imitans* and *J. pellucida* were reared to adulthood on potted tall fescue *Schedonorus arundinaceus* and the number of days between each instar was counted. Instars three and four were combined because of initial difficulty in determining between these stages without removing them from plants, instars were determined with the help of Stockmann *et al.* (2013). There were 10 induviduals for each species, housed separately on single plants.

In order to determine whether the development of *R. imitans* was dependent upon a period of winter diapause (this chapter indicates that the species overwinters as nymphs) six groups of 10 third instar individuals were placed

singly into 500ml containers with potted *S. arundinaceus*. These were then placed in a refrigerator at $\sim 5°C$ and a L6:D18 lighting regimen for a period of 12 weeks to simulate a winter period.

3.3.4 Determining vertical position preference on plants in *R. imitans* and *J. pellucida*

In order to determine the positional feeding preference in *R. imitans* and *J. pellucida*, on the host plant tall fescue, 11 BugDorm-43074F insect rearing cages (32.5 32.5 77.0 cm) cages were set up with 12 individuals of either *J. pellucida* or *R. imitans* per cage. All rearing occurred on single grass plants, which had three nodes of growth. Observations of the numbers of individuals were scored based on their location on the grass stem: **1 - Base**, on the base or below the first node, **2 - Middle** above the first node but below the second, **3 - Tip** above the second node but below the third. There were five cages of *R. imitans* and six of *J. pellucida*. All insects were added at the fourth instar stage. Two observations were made five days apart on the (17th and 22nd April 2014) after two weeks of acclimatisation.

3.3.5 Comparing egg counts between *R. imitans* and *J. pellucida*

In order to compare between the reproductive output of *R. imitans* and *J. pellucida*, as a proximal measure eggs were dissected from specimens collected in July 2011. Egg counts were not possible for all of the dates because the small number of *R. imitans*. In total eight *J. pellucida* were taken on the 14th of July, and seven on the 27th of July 2014. Whereas 10 and five *R. imitans* were taken on these respective dates. It was not possible to make accurate

estimations of reproductive output from laboratory cultures because there was a large proportion of escaped nymphs and dead early stage nymphs, so the egg counts were used as a proximal measure. Total body lengths were taken from head to tip of abdomen, and hind tibia whilst in alcohol to the nearest 0.01 mm.

3.4 Statistical methods

3.4.1 Modelling life cycles

To compare the life cycles of different species, generalised additive models (GAMs) were applied. Models used a three sample moving average number of individuals across three dates. The mean number of individuals three sampling dates, to account for sampling error. Patterns in abundance across different sampling dates were modelled by a cubic smoothing spline (Green & Silverman, 1994). These models were carried out using the R package *mgcv* and the function *gam* (Wood, 2011).

3.4.2 Estimating species richness

In order to estimate species richness for each of the sampling dates a jack–knife method adapted form Burnham and Overton (1978, 1979) was used with the R package *SPECIES* (Wang, 2011). This method utilised the *frequency of frequencies* (FF) in order to compute the species richness and credible confidence intervals for each of the sampling dates. FF is essentially counts of each of the unique samples. For example, species x was sampled 180 times; there were no other species that were sampled 180 times therefore its FF for 180 is 1. In this hypothetical sample there were also 27 singleton species, therefore the FF for 1 is 27.

The average number of species is calculated with the formula (Wang, 2011):

$$\hat{N}_{jk} = D + \sum_{j=1}^{k} (-1)^{j+1} \binom{k}{j} n_j$$

The input data n is defined as a two-column matrix or data frame, where the first column is j and the second column is nj for j = 1, ..., k , this is sorted in ascending order of j. The number of distinct species is denoted D, j is a count and nj the number of species with counts of j.

Species accumulation curves demonstrate how effective a sampling effort is at determining local species richness. The number of species is plotted against a cumulative sampling effort; the acceleration rate of this curve decreases as representative species richness is reached. A rarefaction method was used in this case after Hurlbert (1971), which finds the mean number of individuals, for a given sampling effort. Species richness increases with sample size, and differences may be affected by this. Species richness is then rarefied to the same number of individuals. The R package *vegan* (Oksanen *et al.*, 2013) was used with the command *speccacum* to carry out analysis.

3.4.3 Biodiversity indices

Shannon diversity indices (Shannon, 1948) were used to assess community evenness, as a complementary tool to rank abundance distributions. Shannon diversity index H is calculated:

$$H = -\sum_{j=1}^{k} p_j * lnp_j$$

From this Shannon's equitability index E_H could be derived:

$$E_H = H/H_{max} = H/ln[S]$$

where S is the total number of species in the community, Pi proportion of the total number of individuals. In this case H_{max} is equal to the natural log of S.

3.4.4 Principal components analysis

Principal components analysis (PCA) was used to determine how samples differentiated from each other in terms of their species composition. This enabled a better understanding as to how the Auchenorrhyncha sub-communities were differentiated from each other. In order to do this, the abundance data for each of the species was used for each of the samples taken on Coe Fen in 2011, and the *R* function *princomp* from the *R vegan* library (Oksanen *et al.*, 2013) used to convert variables into principal components which were then visualised using biplots.

3.4.5 Modelling positional preference on plants

In order to model the positional preferences of *R. imitans* and *J. pellucida* on plants a bootstrapping method was used, to correct for the multiple observations within rearing enclosures and the scoring system used for determining positions of insects. This was based on a mean average taken from 10 random observations reiterated 100 times. The *R* script used was designed for the analysis:

data $<-$ c()
for (i in 1:100){
data $<-$ c(data, mean(sample(observed,10,replace=T)))}

Where *observed* is the observed data, as a string of numbers representing the position of each individual insect, and *data* the new string of data with 100 iterations. In order to compare these distributions kernel densities were plotted, in order to compare between the two species a two way chi squared test was used to test the differences in frequencies in the different zones of the plant, base middle and tip.

3.5 Results

3.5.1 The community structure and species richness of Auchenorrhyncha on Coe Fen

In 2011 a total of 7,178 Auchenorrhyncha were collected, with representatives from 46 species. Out of this sample, the majority were Cicadellidae (leafhoppers) or Delphacidae (planthoppers), although far fewer of the latter were collected. Of all these species, six are assigned the official status local, two are nationally scarce, notable A and notable B respectively (Ball, 1986), and *R. imitans*, the focus of this study and the rarest species RDB-K, BAP-2007, England NERC S.41 (JNCC, 2010) (Table 3.5.1).

Table 3.5.1: The numbers of each species sampled on Coe Fen in 2011 and their UK conservation status

Species	Number	UK status
Family Aphrophoridae. (froghoppers/spittlebugs)		
Neophilaenus lineatus (L.)	20	common
Philaenus spumarius (L.)	15	common
Family Cicadellidae (leafhoppers)		
Allygus mixtus (F.)	1	common
Anaceratagallia ribauti (Oss.)	5	local
Anoscopus sp. females	133	
Anoscopus albifrons (L.)	12	common
Anoscopus serratulae (F.)	113	common
Aphrodes makarovi Zachv.	110	common
Arthaldeus pascuellus (Fall.)	2431	common
Athysanus argentarius Metc.	16	Notable B
Cicadella viridis (L.)	6	common
Cicadula quadrinotata (F.)	75	common
Cosmottetix caudatus (Fl.)	1	Notable A
Deltocephalus pulicaris(Fall.)	139	common
Doratura stylata (Boh.)	4	common
Elymana sulphurella (Zett.)	4	common
Empoasca decipiens Paoli.	2	common
Errastunus ocellaris (Fall.)	1	common
Eupteryx aurata (L.)	62	common
Eupteryx notata Curt.	2	common
Eupteryx urticae (F.)	56	common

Continued on next page

Species	Number	UK status
Euscelis incisus (Kbm.)	511	common
Macrosteles sp. females	135	
Macrosteles sexnotatus (Fall.)	24	common
Macrosteles variatus (Fall.)	2	local
Macrosteles viridigriseus (Edw.)	36	common
Macustus grisescens (Zett.)	2	common
Megophthalmus scanicus (Fall.)	26	common
Mocydiopsis attenuata (Germ.)	11	common
Psammotettix sp. females	68	
Psammotettix cephalotes (H-S)	42	
Psammotettix confinis (Dahl.)	7	
Recilia coronifer (Marsh.)	1	common
Rhopalopyx adumbrata (C.Shlb.)	2	local
Streptanus sordidus (Zett.)	262	common
Zyginidia scutellaris (H.-S.)	971	common
Family Delphacidae (planthoppers)		
Criomorphus albomarginatus Curt.	3	common
Dicranotropis hamata (Boh.)	4	common
Eurybregma nigrolineata Scott.	2	local
Hyledelphax elegantula (Boh.)	5	common
Javesella dubia (Kbm.)	270	common
Javesella pellucida (F.)	1203	common
Kosswigianella exigua (Boh.)	13	local
Megamelodes quadrimaculatus (Sign.)	10	local
Muellerianella fairmairei (Perr.)	111	common

Continued on next page

Species	Number	UK status
Ribautodelphax imitans (Rib.)	226	RDBK, BAP-2007 England NERC S.41
Stenocranus minutus (F.)	22	common

Within the Auchenorrhyncha community of Coe Fen fewer than 15 species could be considered abundant, with most other species recorded in less than 25 samples through the season. *Ribautodelphax imitans* however, was one of the more abundant species ranking seventh out of all Auchenorrhyncha recorded. The Shannon equitability index was 0.6, with rank abundance distributions illustrating that percentage abundances were typically low for most species [less than 1%]. The plots, however, show normal species rank distributions illustrated by the moderate decline in log abundance with increasing rank. Approximated slopes for all combined species, Delphacidae and Cicadellidae were -0.16 (Fig 3.5.1) respectively. *Arthaldeus pascuellus* (Cicadellidae) was more abundant (2431) than the dominant delphacid *J. pellucida* (1203), 33.9% and 16.8% of total Auchenorrhyncha respectively, compared to *R. imitans* with $\approx 3\%$ of the total catch.

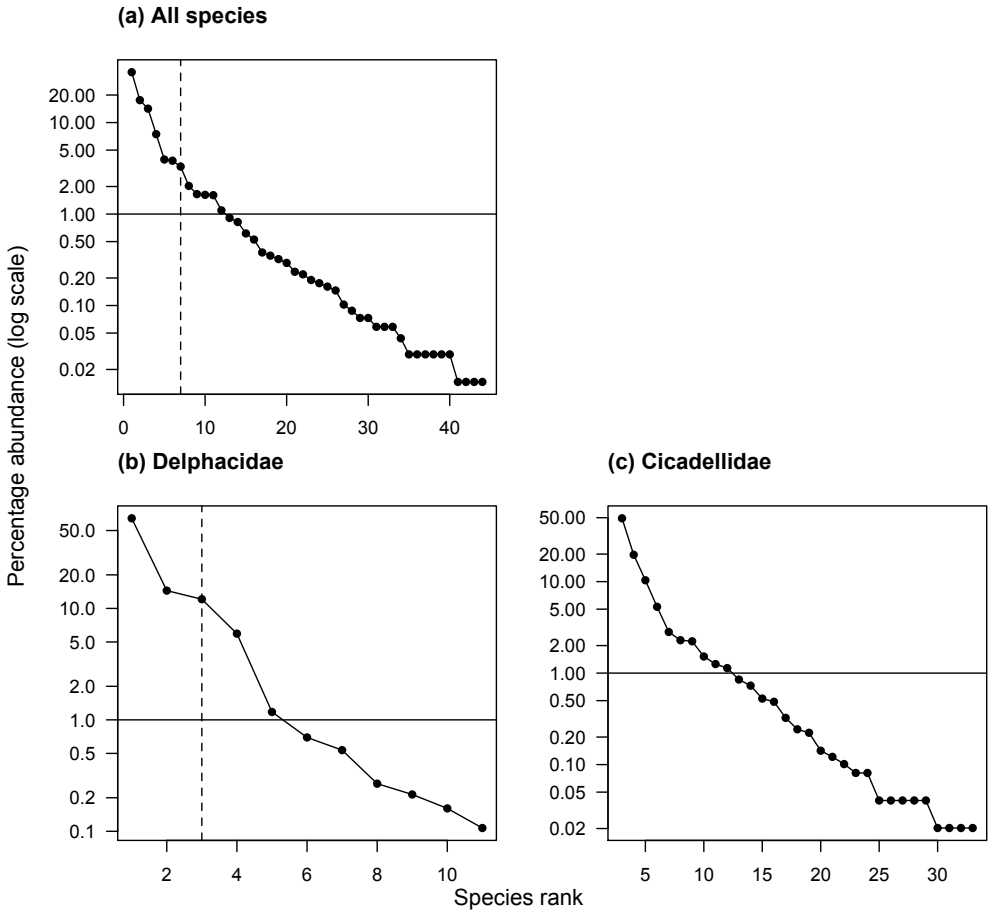

Figure 3.5.1: Rank abundance diagram or Whittaker plot (Whittaker, 1972): Log percentage abundance by rank of all Auchenorrhyncha in the study (a) followed by only Delphacidae (b) and Cicadellidae (c). Vertical dashed lines show the rank position of *R. imitans*.

3.5.2 Mapping

Out of the 1,765 10km^2 previous records submitted to the scheme, only 376 of these areas received more than 50 records. The majority of 10km^2 squares

have less than 100 records (1,549) most of these less than 50 (1,380) (Figure 3.5.2).

The highest number of records submitted, were from Dorset, Hampshire, Greater London and Kent regions, since the start of this study two new records of *R. imitans* in Cambridgeshire have been found by one recorder more intensively looking for delphacids (pers. comm.), where Records of *R. imitans* were received (226 individuals) (Figure 3.5.2). The high density locations not coinciding in all cases with the records of *R. imitans* (Table 1.4.1)

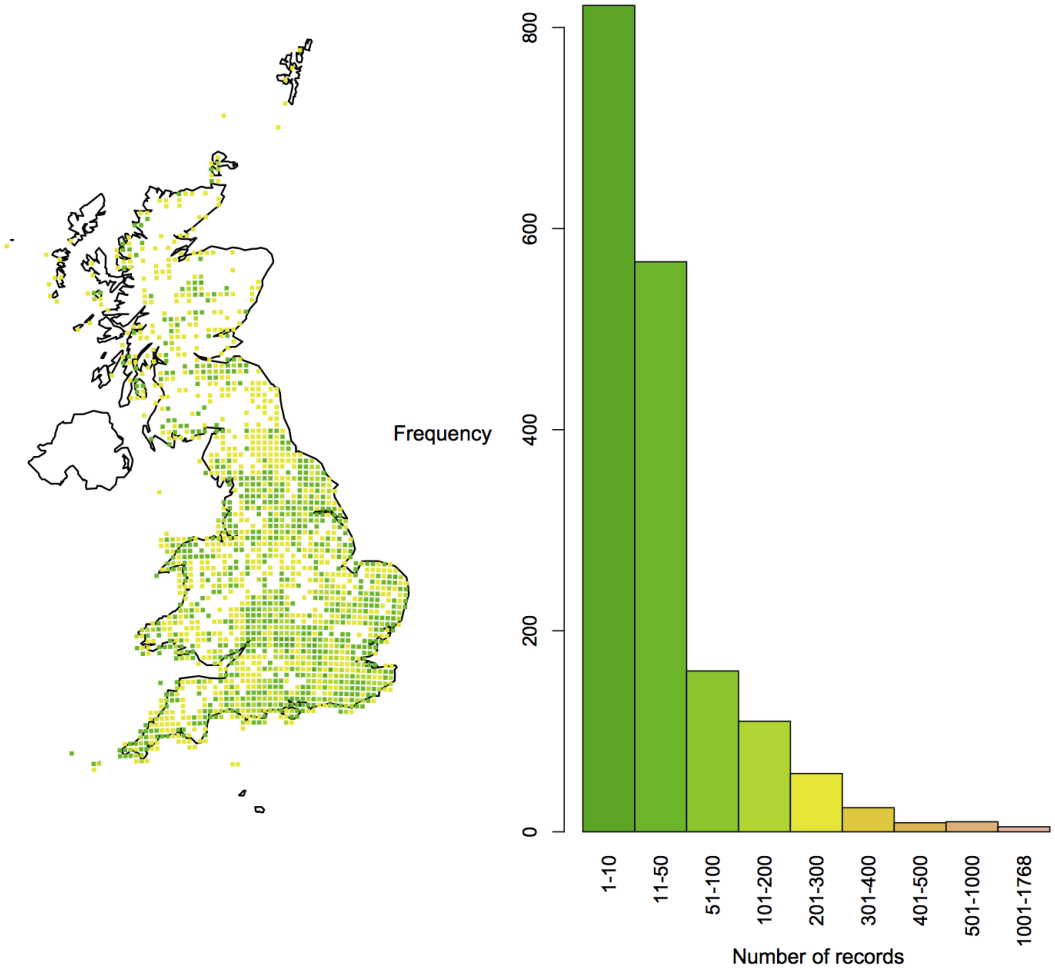

Figure 3.5.2: Map of records from the UK Auchenorrhyncha recording scheme, colours represent numbers of records from each 10 km^2 square. The adjacent chart shows binned frequencies of numbers of records for each 10 km^2 square, the x–axis labels represent the bins for number of records received and y–axis frequency of those bins. The recording scheme for UK, excluding Northern Ireland has a total of 82,593 records (Stewart & Bantock, 2015).

If the Coe Fen community is is typical within the UK, the national ratios of *J. pellucida* to *R. imitans* should be 5.3:1 (looking at the total numbers from 2011 data), whereas ratios of 27.4:1 were submitted to the Auchenorrhyncha Recoding Scheme, significantly different from the ratios in the Coe Fen study ($\chi^2 = 53.17, df = 1, p < 0.001$).

3.5.3 Species richness

It is clear that the number of species sampled reached a peak, from June to mid–August before tailing off (Figure 3.5.3 a). Just five species were recorded at the very start of the field season, and 12 at the end whereas at the peak 30th June 2011, 31 species were recorded. This richness however appeared to drop in July for one of the sampling dates before rising again (Figure 3.5.3 a). Species richness appeared asymptotic with cumulative sampling effort. By 470 samples (9,339 individuals) there was a predicted species richness of 44.6 (95% CI =44.5, 44.7) very close to the final number of 46 species (Figure 3.5.3 b)

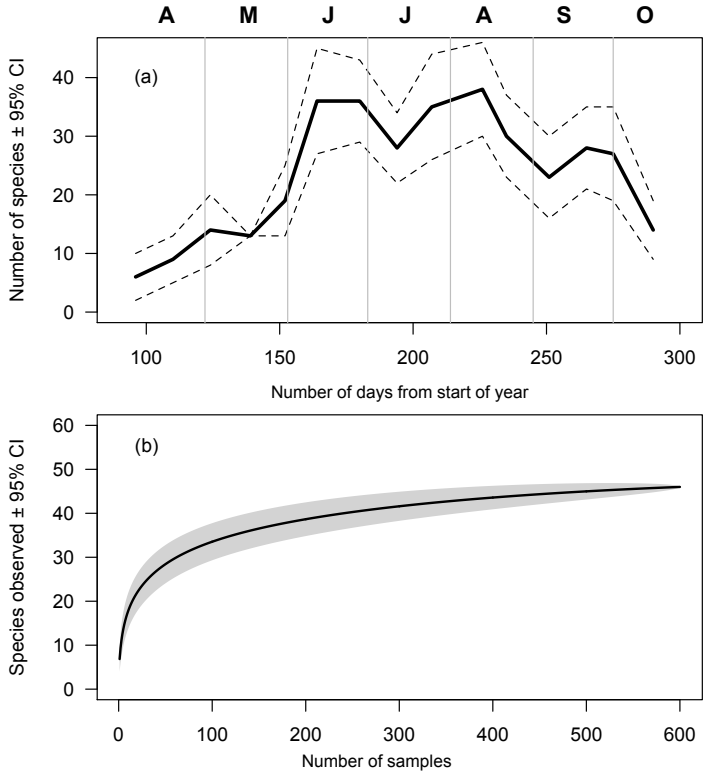

Figure 3.5.3: Species richness for Coe Fen. (a) Species richness and 95% confidence intervals, for each of the sampling dates (b) Cumulative species richness and 60% confidence intervals as a function of the number of samples.

3.5.4 The life cycles of Auchenorrhyncha on Coe Fen

The sampling illustrated differences in life-cycles between the two main groups of Auchenorrhyncha. Delphacids had a June-July peak ($F_{7,8} = 17.40, R^2 = 0.91, P < 0.001$) whereas cicadellids had a July-August peak population ($F_{7,8} = 51.45, R^2 = 0.97, P < 0.001$). With smaller peaks approximately eight weeks previous in each group (Fig. 3.5.4).

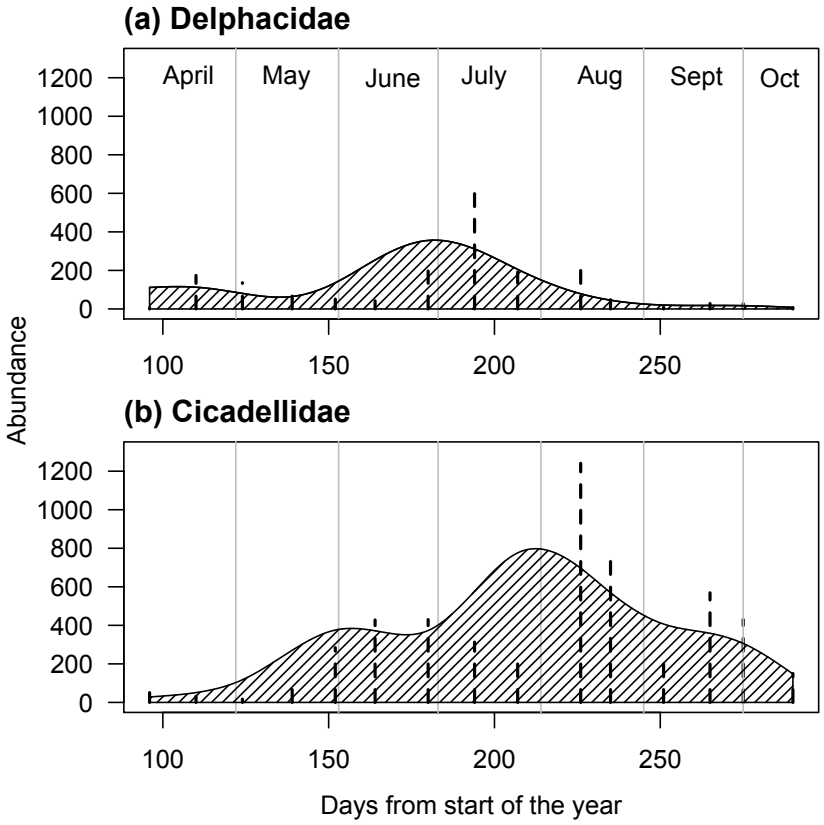

Figure 3.5.4: Raw abundance of Delphacidae (a) and Cicadellidae (b) at each of the sequential sampling events (vertical bars) transposed over the line predicted by the GAM (shaded area).

The life cycle of *R. imitans* appears to mirror that of other delphacids (Fig 3.5.5 a). In 2011 it had two peaks; an early small peak in April followed by a larger peak in June–July (Figure 3.5.5). At the earlier peak 12 individuals were sampled (21st April 2011), and at the late peak 91 individuals were found (14th July 2011), a three sample average abundance of 9 and 48 respectively. The shape observed with the smoothed average when fitted

with a GAM was significant, and conformity to the line high; an explained deviance exceeding 92% ($F_{7,8} = 19.13, R^2 = 0.92, P < 0.001$) (Figure 3.5.5 a).

The life cycles of the other nine most abundant Auchenorrhyncha were also modelled. The profiles of each species are given in figure 3.5.5, with the significance values of the fitted GAM provided after each species in parenthesis; (b) *Javesella pellucida* ($F_{7,8} = 16.94, R^2 = 0.91, P < 0.001$) (c) *Arthaldeus pascuellus* ($F_{9,6} = 107, R^2 = 0.99, P < 0.001$) (d) *Zyginidia scutellaris* ($F_{8,7} = 19.86, R^2 = 0.92, P < 0.001$) (e) *Javesella dubia* ($F_{6,9} = 9.87, R^2 = 0.83, P = 0.002$) (f) *Euscelis incisus* ($F_{8,7} = 69.3, R^2 = 0.98, P < 0.001$) (g) *Muellerianella fairmairei* ($F_{7,8} = 8.60, R^2 = 0.83, P < 0.001$) (h) *Anoscopus serratulae* ($F_{8,7} = 16.50, R^2 = 0.91, P < 0.001$) (i) *Streptanus sordidus* ($F_{8,7} = 109.70, R^2 = 0.99, P < 0.001$) and (j) *Deltocephalus pulicaris* ($F_{8,7} = 23.31, R^2 = 0.93, P < 0.001$).

Each species that was modelled had at least one generation from April to October. Most species had two generations a year, with the exception of *Zyginidia scutellaris*; which appeared to have three generations, and *Anoscopus serratulae*; which had just the one. *Euscelis incisus* had the earliest peak of all, with 51 individuals caught on the first sampling day. It was the earliest maturing of all the abundant ranking species caught.

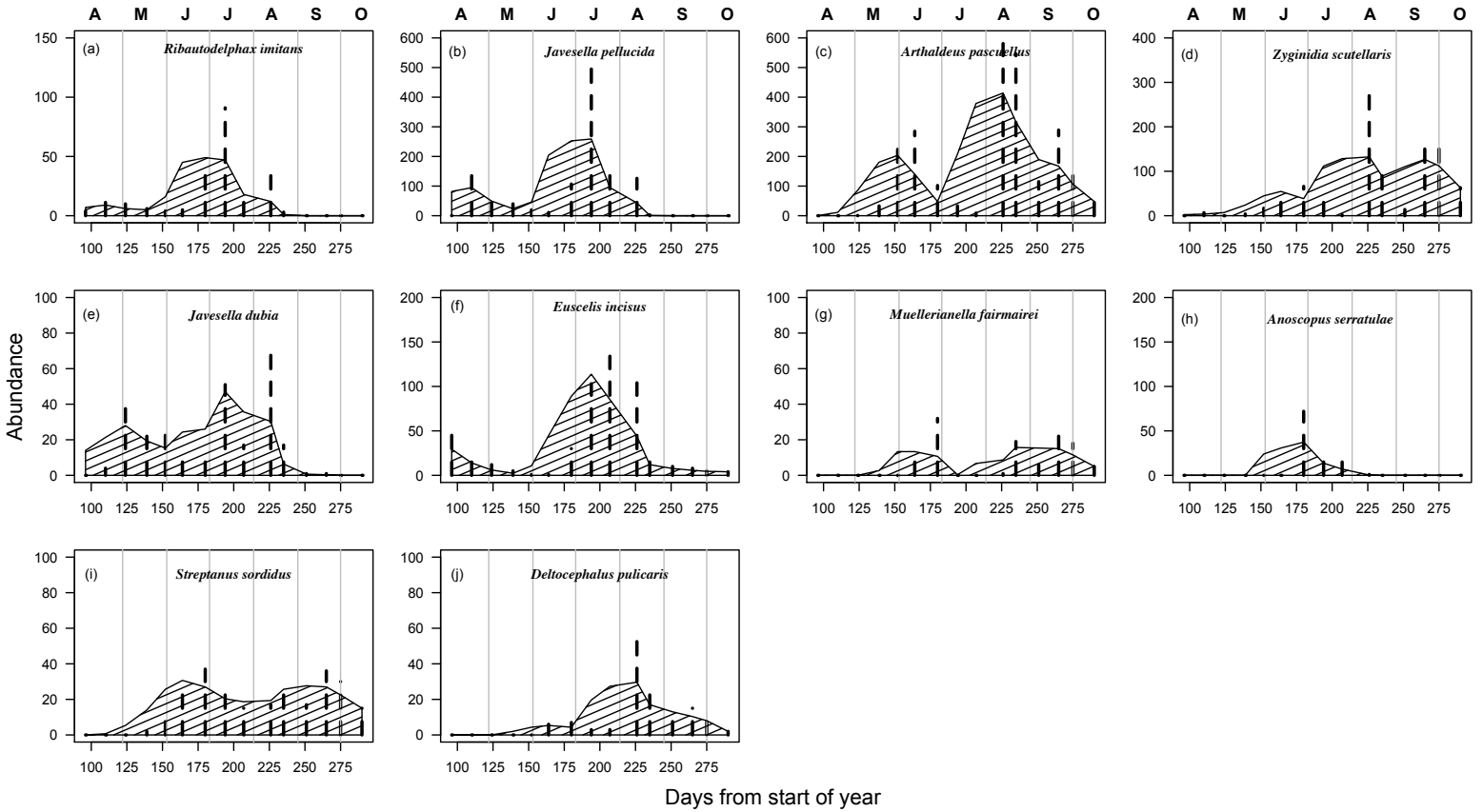

Figure 3.5.5: The life cycles of 10 of the most abundant Auchenhorryncha on Coe Fen represented as the number of individuals recorded at a given date. Dashed vertical lines represent the raw data, and the solid hatched area the line fitted from the GAM. The letters above the graphs represent the months A: April – O: October.

Ribautodelphax imitans and *J. pellucida* were most similar in terms of their life cycles (Figure 3.5.5 a, b). Male to female sex ratios of *R. imitans* and *J. pellucida* were also similar both within and between species; 112:114 and 591:612 respectively, approximate 1:1 ratios. Moreover, there appeared to be no difference in the times in which males and females of either species appeared in the field (Figure 3.5.6).

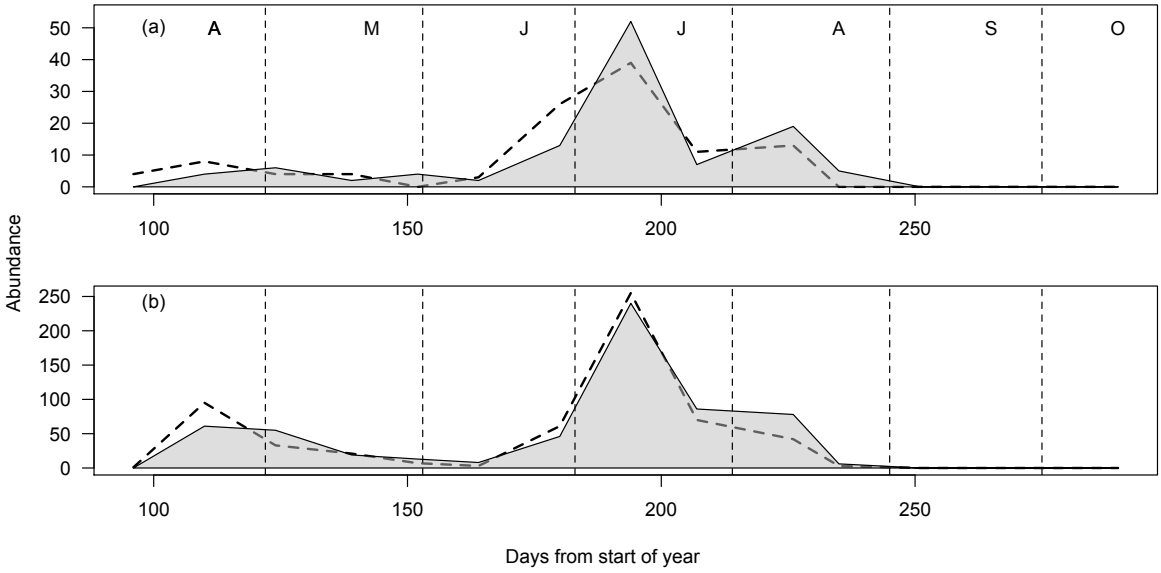

Figure 3.5.6: Phenogram, showing the the differences between male (dashed lines) and female (grey shaded area) presence in the field. (a) *R. imitans* and (b) *J. pellucida*. The letters above the graphs represent the months A: April – O: October.

3.5.5 Community structure

Principal components analysis was used to determine species specific differences in community composition. It was clear from the analysis (Figure 3.5.7) that *J. pellucida*, *Z. scutellaris*, *E. incisus* and *A. pascuellus* were most dissimilar in samples from the rest of the species. *Ribautodelphax imitans* appeared to order along the same axis as *J. pellucida* and *E. incisus* suggesting more community similarities between the samples containing these species in terms of their species composition than others (Figure 3.5.7). The first principal component explained 56% of the variance in the model, and 95% was explained by the first six (of 19) principal components.

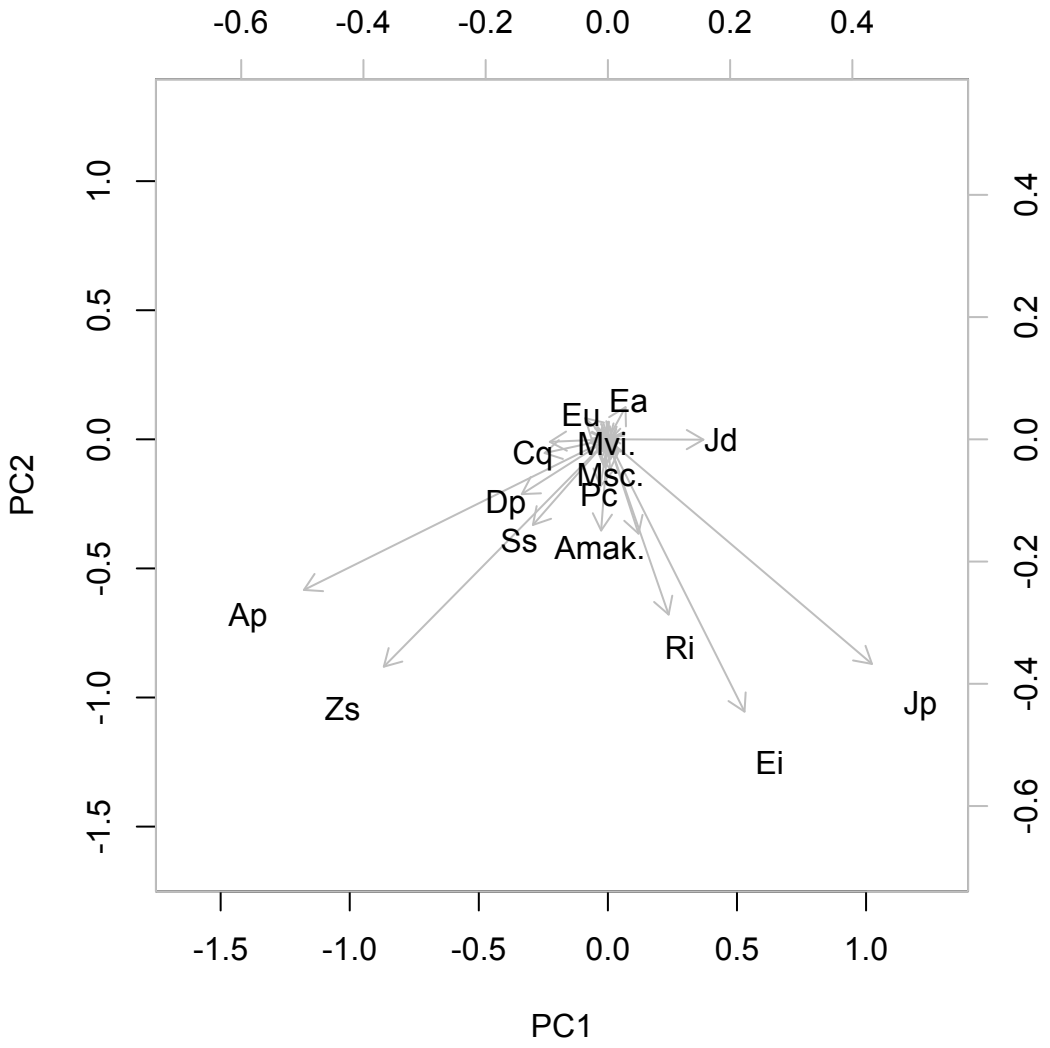

Figure 3.5.7: A principal components analysis of the Auchenorryncha community on Coe Fen. Only those species with the top 14 highest ranking PCA scores are shown on the plot, in order for the plot to be clearly interpreted. Ri *Ribautodelphax imitans*, Jp *Javesella pellucida*, Jd *Javesella dubia*, Ei *Euscelis incisus*, Ap *Arthaldeus pascuellus* and Zs *Zyginidia scutellaris*, Ss *Streptanus sordidus*, Pc *Psammotettix cephalotes*, Dp *Deltocephalus pulicaris*, Cq *Cicadula quadrinotata*, Eu *Eupteryx urticae*, Ea *Eupteryx aurata*, Amak *Aphrodes makarovi*, Msc. *Megopthalmus scanicus*, Mvi. *Macrosteles viridgriseus*.

3.6 Laboratory development of *R. imitans* and *J. pellucida*

3.6.1 Development times

The eggs of *R. imitans* hatched after 19 days (95% CI = 16, 22). GLMs illustrated that in the laboratory *R. imitans* development took markedly longer than *J. pellucida* (Table 3.6.1; Figure 3.6.1). *Javesella pellucida* and *R. imitans* in the wild both had approximately 84 days between adult generations (Figure 3.5.5 a and b; Figure 3.5.6). In the laboratory contrasting patterns were observed. *J. pellucida* reached adulthood following 27 days (95% CI = 23,31) as nymphs. *Ribautodelphax imitans* took a markedly longer and more variable period of time; a mean of 72 days, (95% CI = 41,102) albiet with a large range; a significant difference of 44 days (95% CI = 14,74) between the total laboratory development time of *R. imitans* and *J. pellucida* ($t_{23} = 3.74, p = 0.012$, figure 3.6.1 d). The skew associated with *R. imitans* development was much greater than observed with *J. pellucida* however neither were significantly different from a normal distribution (Shapiro-Wilk: *J. pellucida*, $W = 0.080, p = 0.066$; *R. imitans*, $W = 0.838, p = 0.125$).

From the first to second instar *R. imitans* developed markedly slower than *J. pellucida* (Figure 3.6.1 a; Table 3.6.1 a) but by the second to third instar stage this pattern was reversed (Figure 3.6.1 b; Table 3.6.1 b). In terms of both the duration between the third instar to adult stage, which was the longest period between instars in *R. imitans*, there was also an effect of sex with males of *R. imitans* (but not *J. pellucida*) developing more slowly than females in both this life stage and their total development times (Table 3.6.1 c, d). Males were predicted to develop in 72.1 days (95% CI = 28.8, 191.1) compared to females which were predicted at 45.5 days (95% CI =

18.1, 113.7) significantly faster than females, but with a large overlap in confidence intervals between the sexes ($Z_{16} = 3.60, p < 0.001$).

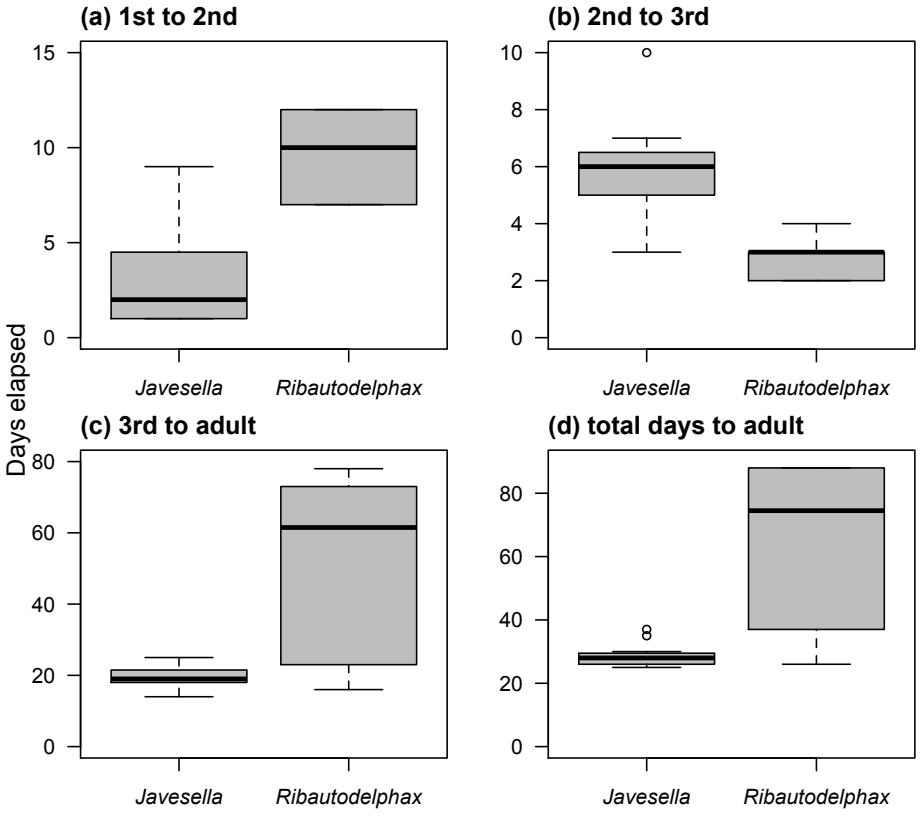

Figure 3.6.1: The total number of days elapsed from first instar nymph to adulthood (a) from first to second instar (b) from second to third (c) and from third to adulthood (d). There is no 3rd to 4th instar duration because of difficulty in determining between these stages.

Experiments which looked at the development of third instar *R. imitans* following a period of simulated winter diapause showed that this period of cooling did not expedite development. After a period of 56 days following

Table 3.6.1: Generalised linear models showing the developmental times between different instars (a) 1–2 (b) 2–3 (c) 3–adult (d) total time to adulthood. *Javesella pellucida* is taken as the intercept value for all factors against *R. imitans* (RI), and M (males) is compared against the intercept value for female, Par. est, is an abbreviation for parameter estimate, colons ':' denote interactions between terms. Models a and b have 21 degrees of freedom c and d 16 degrees of freedom, and the AIC values for a=112.47, b=88.41, c=157.01, d=161.25. All models used a Poisson error structure and log link between the parameter estimate and the mean of the distribution.

Coefficient	Par. est.	95% CI	SE	Z	p
(a) (Intercept)	1.299	1.004, 1.595	0.151	8.618	< 0.001
Species RI	0.983	0.627, 1.339	0.181	5.417	< 0.001
(b) (Intercept)	1.720	1.480, 1.959	0.122	14.077	< 0.001
Species RI	-0.588	-1.014, -0.163	0.217	-2.709	0.007
(c) (Intercept)	3.060	2.887, 3.234	0.088	34.623	< 0.001
Species RI	0.481	0.188, 0.773	0.149	3.219	0.001
Sex M	-0.215	-0.489, 0.058	0.139	-1.545	0.122
Species RI : Sex M	0.785	0.403, 1.167	0.195	4.027	< 0.001
(d) (Intercept)	3.401	3.255, 3.547	0.075	45.632	< 0.001
Species RI	0.417	0.164, 0.669	0.129	3.238	0.001
sex M	-0.105	-0.329, 0.118	0.114	-0.925	0.355
Species RI : sex M	0.595	0.271, 0.919	0.165	3.600	< 0.001

the experiment only two of *R. imitans* had developed into adults. At this point experiments were terminated, as it was concluded that the effect of diapause on nymphs (if any) was less than any difference between the two species in their developmental times. They still spent markedly longer in the third instar to adult stage.

3.6.2 Positional preferences of *J. pellucida* and *R. imitans*

Positional preferences of *R. imitans* and *J. pellucida* were significantly different from each other in laboratory cultures ($\chi^2 = 69.86$, df = 2, $p < 0.001$). *Javesella pellucida* had a distinct preference for the middle section of plants, whereas *R. imitans* more towards the mid and tip regions (Figure 3.6.2).

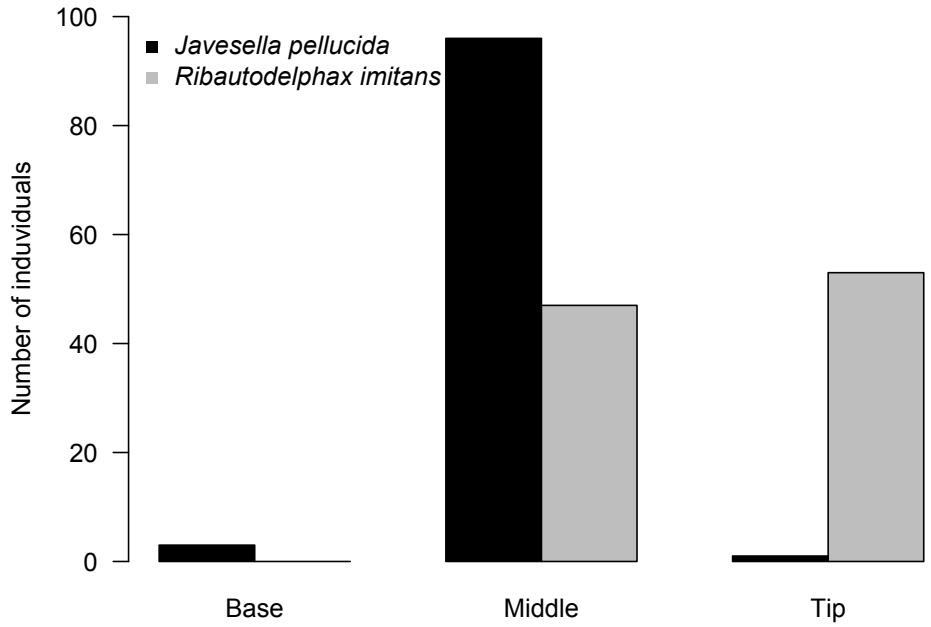

Figure 3.6.2: The positional preferences on tall fescue plants of *J. pellicida* and *R. imitans* **Base**, on the base or below the first node, **Middle** above the first node but below the second, **Tip** above the second node but below the third.

3.6.3 Estimating egg burden of *R. imitans* and *J. pellucida*

A mean of 15.3 (95% CI = 12.8, 17.7) eggs were dissected from the abdominal cavities of *J. pellucida* whereas *R. imitans* samples contained a mean of 7.4 (95% CI = 5.7, 9.0) eggs. A mean difference of 7.9 (95% CI = 7.4, 15.3) between the species ($t_{25} = 5.7, P < 0.001$). There were no differences between the number of eggs in insects sampled on different dates (Figure 3.6.3). Of the 15 *R. imitans* sampled 80% of them were brachypterous wing

forms and of the 15 *J. pellucida* 44% were brachypterous. There was no significant difference in egg counts between wing forms for either *R. imitans* ($t_{14} = -0.33, p = 0.750$, mean difference = -0.60 [95% CI =$-4.94, 3.738$]), or *J. pellucida* ($t_{14} = 0.0196, p = 0.986$, mean difference = 0.08 [95% CI = -15.99, 16.16]).

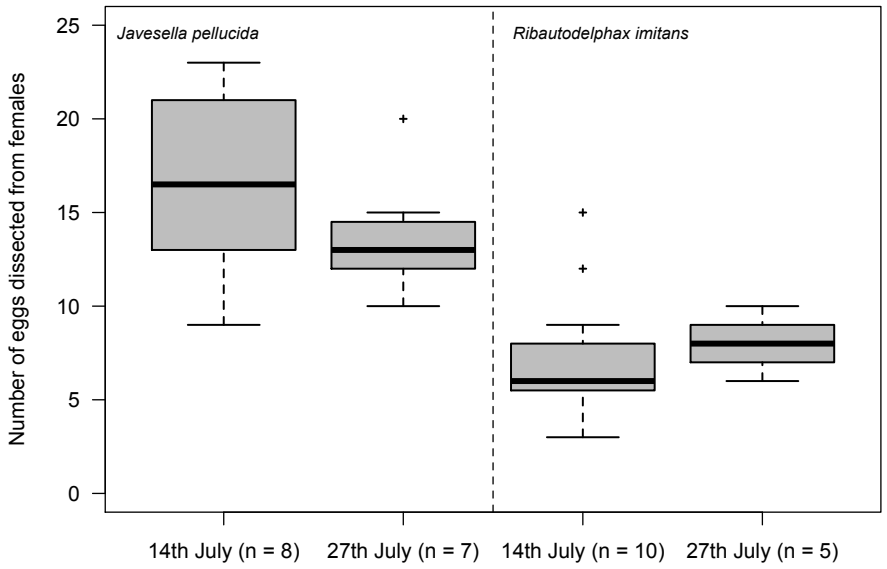

Figure 3.6.3: Difference between the egg counts from female *R. imitans* and *J. pellucida* on different sampling dates for the July peak abundance in 2011.

There was no significant relationship between the total body length of (from head to tip of abdomen) (*R. imitans*: $F_{1,10} = 0.074, p = 0.791, R^2 = 0.09$, or *J. pellucida*: $F_{1,6} = 2.118, p = 0.196, R^2 = 0.20$) and the number of eggs dissected from females. There was no significant effect detected between hind

tibial length and the total egg counts ($F_{1,18} = 3.466, p = 0.079, R^2 = 0.11$, figure 3.6.4 b).

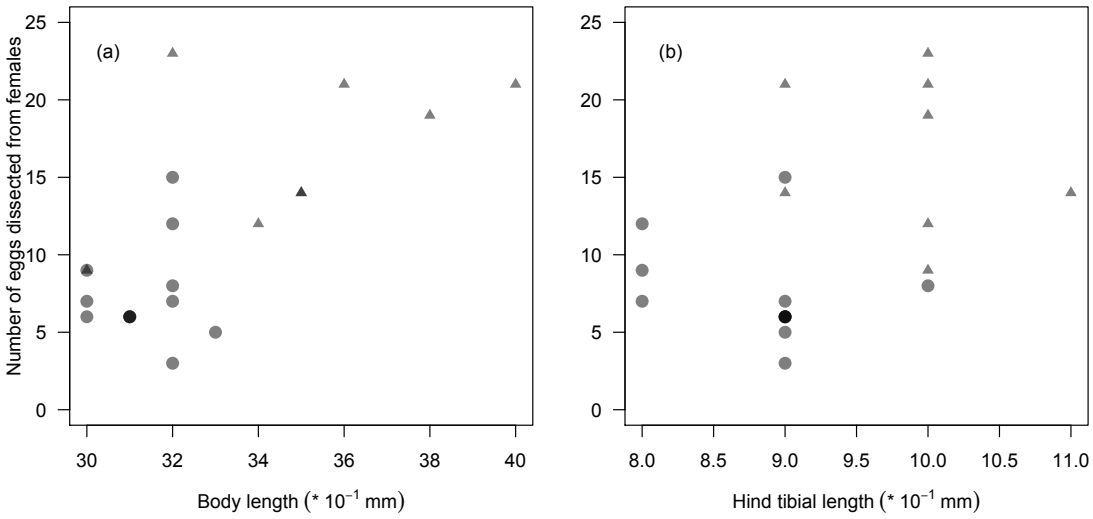

Figure 3.6.4: The relationship between the total body length of individuals (a) or the hind tibial length (b) and the number of eggs dissected from the abdomens of females. Circles show *R. imitans* and triangles *J. pellucida*. The darkness of the colour is indicative of overlapping points.

Eggs did not vary in size between species ($t_{20} = 1.393, p = 0.187$) they had a mean volume of 0.75mm^2 (95% CI = 0.72, 0.77, $n = 20$)[1]. Field samples of *R. imitans* were a mean body length of 3.13mm long (95% CI = 3.07, 3.19), whereas *J. pellucida* were a mean of 3.50mm (95% CI = 3.24, 3.76); significantly longer by 0.37mm (95% CI = 0.10, 0.63) ($t_{24} = 3.178, p = 0.013$) measured from the tip of the head to tip of the abdomen.

[1]eggs were cylindrical and approximately 0.10mm in cross section, volume was estimated using this measurement and length (0.10mm x length)

In addition there was a significant difference in the total lengths of laboratory cultured *J. pellucida*. Compared to their wild counterparts cultured specimens were an average of 0.3mm (95% CI = 0.02, 0.57) smaller ($t_{17} = 2.436, p = 0.035$). However, there was no significant difference in the laboratory cultured and wild *R. imitans* total lengths ($t_{23} = 0.735, p = 0.472$).

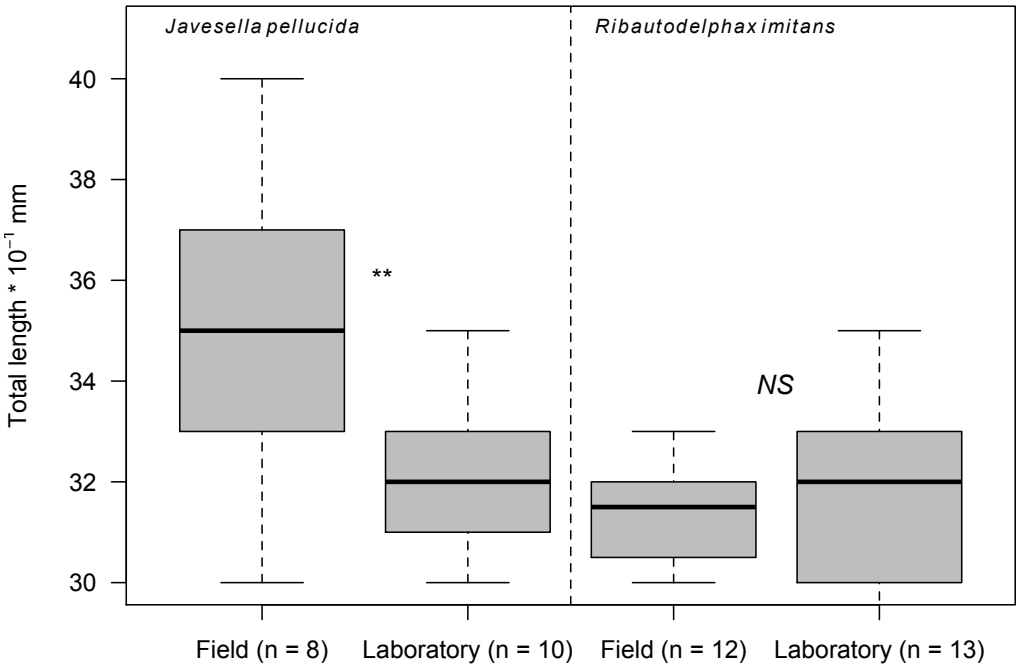

Figure 3.6.5: The body lengths of (a) *J. pellucida* and (b) *R. imitans* in samples from field and laboratory cultures. ** Denotes statistically significant results, NS no significance

3.7 Monitoring of the site

3.7.1 Interspecific relationships

When the species abundance data were investigated from 2011 to 2014 there were correlations between *R. imitans* and *J. pellucida* adults ($F_{1,6}, P = 0.03, R^2 = 0.48$, Figure 3.7.1). There was no significant relationship between *R. imitans* and *J. dubia* (Y = 0.01x + 9.62, $F_{1,6} = 0.001$, $p = 0.99$, $R^2 = 0.00$), *Z. scuttellaris* (Y = - 0.05x + 10.79, $F_{1,6} = 0.289$, $p = 0.631$, $R^2 = 0.00$) and *E. incisus* (Y = - 0.05x + 7,91, $F_{1,6} = 0.526$, $p = 0.496$, $R^2 = 0.00$). There were no other species that were abundant enough (recorded mostly as single specimens) or occurred on enough dates (less than four) at the same time as *R. imitans* to carry out individual regressions, the full data is in appendix 1, table A1.

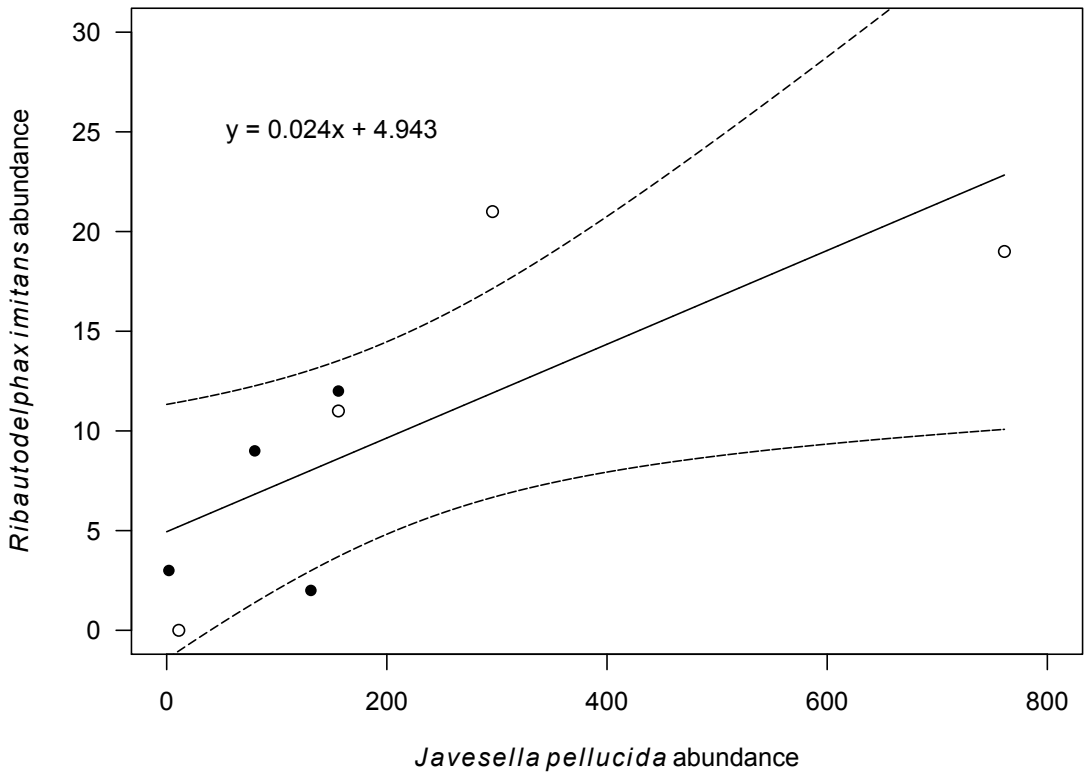

Figure 3.7.1: The relationship between the numbers of *J. pellucida* and *R. imitans*. Samples taken twice a year April and July, from April 2011 to April 2015. Solid circles show April measurements and July are open circles. Dashed lines show 95 percent confidence interval. There was no April 2012 sample, as sampling could not be conducted in bad weather.

3.8 Discussion

3.8.1 Life cycle and status of *R. imitans*

This chapter supported a previously found pattern of asynchrony between delphacids and cicadellids (Waloff, 1979, 1980; Nickel, 2003) in line with the hypotheses. This may be an important factor in reducing competition, between related delphacids and cicadellids (Waloff, 1979, 1980). *Javesella pellucida* was the most abundant delphacid on the site co–abundant year to year, and seasonally synchronous with *R. imitans* therefore studies of competition between these two species could elucidate community interactions, competition or possibly facilitation. Lab based experiments demonstrated that there were some differences between the two in terms of both their developmental times and their position on plants, supporting the hypotheses.

These species' overlapping generations could indicate interactions but it is unknown as to whether there is any direct competition between the two species which affect population sizes. Synchronous generations could increase the chance of direct competition. Phenology can reduce competition between species if life-cycles are asynchronous (Dudley *et al.*, 1990). This balance is sensitive, because life cycle synchrony can be altered by climate change; which can lead to an uncoupling of important relationships, such as the co-occurrence of insects and their host plants (a trophic mismatch) (Edwards & Richardson, 2004). However this is potentially more important when one species is reliant upon the other, like with pollinators and plants (Kudo & Ida, 2013). Auchenorrhyncha are generally less dependent upon seasonally fluctuating food sources, such as flowering buds (Biedermann *et al.*, 2005; Nickel & Remane, 2002; Nickel, 2003; Nickel & Hildebrandt, 2003). There are some exceptions with Hemiptera, aphrophorid bugs feeding on Asteraceae

flowerbuds, sometimes compete with lepidopterans (Karban, 1986). If there is a trophic mismatch this can lead to asymmetric competition where the division of resources is not equal (Karban, 1986). Therefore, phenology is important because understanding more about the interactions between those species that overlap and those that do not informs understanding of how interactions drive community structure; it builds a better understanding of why some species, such as *R. imitans*, are rare.

Within communities, species may not be numerically abundant; indeed the majority of species are rare when compared to the dominant few, but are they truly rare? In this study *R. imitans* is a potential example of one species that is locally abundant (albeit not dominant) but restricted in some way, as indicated by the lack of national records for this species. However, the exact reasons for the rarity of *R. imitans* are unknown. Rarity is commonplace all over the animal kingdom, but the reasons behind persistence of rare species through space is not easily explained. Potentially rare species persist if their environment is ecologically stable (Harrison *et al.*, 2008) and because of their specificity or range limitations, their population sizes can be restricted leading to localised rarity (Rabinowitz *et al.*, 1986). Some species are highly specialised, requiring a subset of habitat characteristics in order to persist; for example these can require specific habitats, host plants, growth phases or the microclimate that the plant provides (Inbar & Wool, 1995; Ali & Agrawal, 2012). In the case of *R. imitans* host plant drivers are unlikely to be the cause of rarity, because its host plant *S. arundinaceous* is not rare (den Bieman, 1987) (Chapters 4 and 5). Species can also be rare because geographically they are at the edge of their range, at the limit of their ecological tolerances (Goulson *et al.*, 2005). The overlapping adult generations and delphacid community dominated by *J. pellucida* could however suggest

rarity driven by interspecific interactions. Conversely, ratios of the numbers of *R. imitans* when compared to the numbers of submissions to the national Auchenhorryncha recording scheme (Stewart & Bantock, 2015) suggesting it is either rarer nationally than on this local scale or that national recording efforts are insufficiently intense to detect this rare species.

3.8.2 How does *R. imitans* relate to other species in the community?

Javesella pellucida is the most abundant (see introduction chapter) delphacid on the study site, and widespread throughout the UK. *Ribautodelphax imitans* although relatively abundant on this site, it is still much rarer than *J. pellucida* (the ratios of the species to each other are 5.4:1). There were differences in approximate egg load between *J. pellucida* and *R. imitans* which could have contributed to the population sizes of each of these species. Relationships between body size and the number of eggs found in abdomens could be attributed to the lower outputs of *R. imitans*, because the species is significantly smaller. A species could negate this by having smaller and more numerous eggs (Honěk, 1993), although there were no differences between the two species. Whether egg load alone is enough to explain differences in population size is unlikely, as the magnitude in difference was not proportional to the two species populations size. Differences in population size can be related to the population dynamics of the two species, including combinations of factors such as fecundity, mortality and migration, and factors interacting with these processes such as predation (Wallner, 1987).

The observation that populations of *R. imitans* are correlated with *J. pellucida* could potentially indicate community interactions, however the large variability in the data could suggest circumstantial effects. If the species

were competing directly then a simple hypothesis stating that one population was suppressed by the other would be supported by a negative relationship. Population sizes can be checked by both direct and indirect competition between conspecifics and allospecifics (Denno & Kaplan, 2007; Kaplan & Denno, 2007). However, the relationship between abundance, suggests one of two things; it is possible that the species are dependent upon each other in some way, however they may just both be responding to the same biotic or abiotic environmental variables that fluctuate year on year, which is most likley.

Mechanisms underpinning this relationship warrant further investigation. It is possible it is a case of plant phenology or environmental factors driving similarities in these two species. Plant phenology is clearly important in herbivorous insect development, particularly through its relationship with plant quality (Prestidge & McNeill, 1983; Mopper & Simberloff, 1995; Awmack & Leather, 2002). Also important are external factors such as temperature (Bale *et al.*, 2002). However, the idea that *R. imitans* is facilitated by *J. pellucida* should not be discounted. Further investigations are needed, in order to elucidate what the main drivers behind co-abundance patterns are. Earlier feeding by some species can facilitate the performance of others in rare cases, such as chewing guilds in which the new growth after grazing may provide an enriched food source for other herbivores (Damman, 1989); there are some examples between sucking guilds, in particular between planthoppers (Cao, Backus, Lou & Cheng, 2013; Cao, Lü, Lou & Cheng, 2013), although in these cases the measured responses could be indicative of altered plant chemistry which increased the amount of feeding. The honeydew produced from the increased volume of phloem ingested then lead to increased atten-

dance by mutualistic ants, which in tern improved growth and survivability (Zhou *et al.*, 2012).

3.8.3 How does the development of *R. imitans* compare to other species?

Generation times of *R. imitans* were much longer than *J. pellucida* in the lab. There were small differences in egg incubation time that could account for the differences observed in the field versus those observed in the lab. The pre-ovipositional stage lasts 5–6 days for *Ribautodelphax* spp. (den Bieman, 1987), so the egg incubation time could be approximated to 14 days using the time the females were added to enclosures and the first nymphs appearing. Oviposition in grass stems was not evident in *R. imitans*. Field data for *J. pellucida* suggests an egg incubation period of approximately 28 days throughout the season. Previous studies of laboratory cultures suggest an incubation duration minimum of 17 days at an average of 17°C (Raatikainen *et al.*, 1967).

The differences observed between two species in the laboratory versus field could indicate that there is something absent in the laboratory that is present in the wild. There were no differences in sizes of *R. imitans* individuals comparing lab cultures to field, however there were with *J. pellucida*. Development times are shortened by increased temperature, within the boundaries of the species' physiology, with higher temperatures leading to faster development but smaller individuals (Reineke & Hauck, 2012). Although the controlled temperature system was calibrated to approximate the UK average temperature over the summer, there were inevitably some differences between the environmental conditions, in-situ and ex-situ, such as light intensity and humidity. However, both species comparisons were made

in the same conditions; therefore any affect of temperature and light would have equally affected both species.

Developmental periods between instars were different for each species, which could indicate that although adult generations were synchronous, the nymphs were not. Different delphacid species can be found at different heights in the sward, showing seasonal habitat preference (Andrzejewska, 1965). Vertical preferences are seen with nymphs in particular, and because of their fragility they have strong microhabitat preferences influenced predominantly by relative humidity (Isichaikul & Ichikawa, 1993) as well as parasite and predator avoidance (Pierce, 1988; Cook & Streams, 1984; Takakura & Yamazaki, 2007) . Although feeding on the same plant, vertical position and preference (as demonstrated in this chapter) mediates direct interactions between species and partitions resources amongst them, negating competition for space to some extent (**?**Ferrenberg & Denno, 2003), however, as they are both phloem feeders, being on different parts of the plant could still result in competition for food. Differences in the developmental times between life stages of the two species could be a positive adaptive trait, because if microhabitat preferences are dependent upon life stage, the two species would, at least whilst sub-adult, be in different microhabitats. However, the laboratory conditions on single plants were quite homogenous, and differences in positional preference less likely to be directly influenced by factors like humidity. Other experiments looking at how different instars behave on host plants, and how positional preferences are mediated by other species could elucidate these differences.

3.8.4 How has the study on Coe Fen improved knowledge of *R. imitans* so far?

The likelihood of encountering *R. imitans* following low intensity sampling would be quite small on any site if similar population densities were to be observed to that on Coe Fen. Life cycles and phenology of species vary year on year, and monitoring any species based on fixed dates (as with management) would not be useful (Nickel & Hildebrandt, 2003; Branson *et al.*, 2006; Blake *et al.*, 2011*b*; Helden *et al.*, 2011; Dittrich *et al.*, 2013; Dittrich & Helden, 2016). Utilising one super-abundant species - such as *J. pellucida* (Dittrich *et al.*, 2013; Dittrich & Helden, 2016) - as a cue to sample another species, is useful when targeting rare species as it could enable shorter, lower intensity preliminary surveys to precede more intensive demographic studies.

Detailed surveying of sites during delphacid peak abundance periods could help return more records for this species, certainly in the UK and potentially in the rest of Europe. The recording area for Auchenorrhyncha in the UK is quite wide, however recording densities were quite low - with the majority of 10km squares having less than 50 Auchenorrhyncha records. Therefore if one in 32 records was a *R. imitans* on Coe Fen, it could be predicted that only a small proportion of 10km squares on the scheme are likely to have yielded *R. imitans* records even if the species was present.

With a new photographic atlas (Kunz *et al.*, 2011) and the publication of a key on the nymphs of Auchenorrhyncha (Stockmann *et al.*, 2013) replacing more fragmented publications with a comprehensive resource in one place, it is possible that UK records will become more accurate and frequent. *Ribautodelphax imitans* nymphs and adults are recognisable and easily differentiated from others, perhaps more so than commoner species. Surveys in similar grassland types in other locations could turn up records for *R. imi-*

tans. However it is simply possible, that low quality (low floristic diversity) meadows, such as Coe Fen, inland are not preferred locations for recording, due to their low overall biodiversity, status and lack of appeal to recorders. Moreover, these habitat types in coastal areas may even prove inaccessible to recorders looking for these species. However, if an effort is to be made to comprehensively map the Auchenorrhyncha fauna of the UK, low floristic value sites, need to be investigated.

3.8.5 Summary

Ribautodelphax imitans although rare nationally is locally common on Coe Fen. It has two generations per year, in common with many other Auchenorrhyncha species. It showed a correlation with *J. pellucida* abundance but these two species showed contrasts in their characteristics, such as egg load, size and developmental times. It is possible that the correlations between the *R. imitans* and *J. pellucida* between years may indicate either interactions between species or a response to similar environmental effects on the two species. Further work to investigate the possible mechanisms that may have given rise to the population correlation need to be explored. The relationship between the two species could be useful in assessing the status of *R. imitans* at other sites.

Part of this chapter was presented at the 7^{th} European Hemiptera Congress and 9^{th} International Workshop on Leafhoppers and Planthoppers of Economic Importance organized by the ÖKOTEAM in co-operation with the University of Graz, Institute of Zoology, 19^{th}–24^{th} July 2015. Travel was funded by a grant from the Royal Entomological Society and a subsequent

paper published in *Entomologica Austriaca* (Dittrich & Helden, 2016; Appendix 2)

Chapter 4

Plant community effects on Auchenorrhyncha: Host plant associations of *Ribautodelphax imitans*

4.1 Introduction

The majority of global insect diversity is herbivorous with species richness driven by divergence in the ovipositional preference of females, the ability to survive on different hosts and other niche constraints (Janz *et al.*, 1994; Sheck & Gould, 1996; Thompson, 1998). The range of plants upon which Auchenorrhyncha can feed exists in a continuum from monophagy where species feed on just the one species of plant, to polyphagy where they feed on a cosmopolitan range of plants across different families. Other species are restricted to a plant genus, closely related genera or a family, and are com-

monly termed oligophagous (Futuyma & McCafferty, 1990; Nickel & Remane, 2002; Świerczewski, 2014; Forister *et al.*, 2015).

Host plant utilisation can be driven by toxicity and digestibility. Cellulose is an organic compound many herbivores have to deal with in order to exploit plants as a food source, but it is not easily metabolised, (Abe & Higashi, 1991). Some insects utilise enzymes to exploit cellulose as a food source, through combinations of cellulases and mutualistic microscopic organisms (Terra, 1990; Martin *et al.*, 1991). In a similar way enzymes can be used to negate plant toxicity in the sap from which Auchenorrhyncha feed. Specialisation towards plants that are toxic to generalists is advantageous, as it excludes potential competitors not adapted to these plant defences, although insects have to manufacture detoxification enzymes at significant metabolic cost (Price, 1997; Krieger *et al.*, 1971). Other costs are incurred through host rarity, a single plant species is harder to locate than a range of plants in a community, but plants that produce high levels of volatile chemicals are potentially easier to find, as the chemical cues are easier to locate by searching insects (Cates, 1980; Price, 1997; Lankau, 2007). However, these same chemicals can also be exploited by predators and parasites notifying them of the presence of prey and host insects (Paré & Tumlinson, 1999). Generalists on the other hand, have potentially more abundant food sources, but are not likely to have any specialised adaptations for dealing with some foods or plant volatiles (Ali & Agrawal, 2012).

The knowledge of the host plants of *Ribautodelphax imitans* were recognised in the BAP as a gap in our understanding of this species, and therefore in need of study (JNCC, 2010). Understanding associations between plants and their herbivores is important, because it enables a greater knowledge of how communities are structured within different habitats. den Biemen

(1987) showed that continental European populations of *R. imitans* were monophagous on tall fescue *S. arundinaceus*. However, host plant relationships in one location are not always the same as in other places. *Ribautodelphax pungens* for example has three different host plants in different parts of its range: *Brachypodium phoencoides, B. pinnatum and B. sylvaticum* (den Bieman, 1987).

It is a commonly held belief that plant diversity mediates insect diversity, to some extent by direct relationships between specialists and their hosts (Maczey, 2005; Novotny *et al.*, 2006; Crutsinger *et al.*, 2006; Helden *et al.*, 2015). However, comunities are not entirely composed of specialists; they are often a complex combination of specialist and generalist species (Waloff & Solomon, 1973; Prestidge & McNeill, 1983; Sedlacek *et al.*, 1988; Novotnỳ, 1994; Littlewood, Pakeman & Pozsgai, 2012; Korösi *et al.*, 2012). In Auchenorrhyncha, plant associations are driven not only by their feeding association, but also by their ovipositional preferences and as a substrate for mating and acoustic communication between sexes (Claridge, 1985; den Bieman, 1985). Understanding these species-specific traits is key to their conservation. This chapter seeks to clarify how host plant networks (the interactions between hosts and consumers) (Dormann *et al.*, 2009) maintain the diversity of Auchenorrhyncha. Moreover, gaining a greater understanding of the relationship between both plant and insect communities, whilst clarifying the host specificity of *R. imitans* in a UK population. It was hypothesised that in line with the Central European literature *R. imitans* is monophagous on *S. arundinaceus* (den Bieman, 1987; Nickel, 2003), but because of the commonness of the plant there would be considerable overlap in the utilisation of it by other species in the field. It was also hypothesised that, a dominance of this plant could theoretically support a large population of *R. imitans*.

4.1.1 Aims

1. Classify the habitat of *R. imitans* on Coe Fen.
2. Clarify the host plant associations of *R. imitans* through a series of choice based experiments.
3. Investigate whether there is any resource overlap between *R. imitans* and other species, particularly the dominant *J. pellucida*, in host plant utilisation.
4. Elucidate the role of the host plant network in maintaining overall Auchenorrhyncha biodiversity.

4.2 Methods

4.2.1 Field-based methods

Synchronised plant and insect surveys were carried out on Coe Fen to assess Auchenorrhyncha diversity. The same methods for insect collection were used as in the general methods section (Chapter 2). In total 40 randomised insect samples (as in the monitoring of Coe Fen) with matched 1 x 1 m (10 x 10 cm divisions) plant quadrats from the same location. Within quadrats all the grass and dicotyledon species present were recorded, and percentage cover was recorded for each species.

4.2.2 Host plant choices of *R. imitans*

Groups of ten individual third instar *R. imitans* were placed in containers with a free choice of one of four plants; tall fescue *S. arundinaceus*, Yorkshire

fog *Holcus lanatus*, creeping bent *Agrostis stolonifera* and cock's foot *Dactylus glomerata*. The plants were grown in small 5 cm diameter plugs in John Innes no.3 potting compost, at a density of about 10 seeds per plug, placed in a tray 15x10cm, in sealed perforated polythene bags (Clear PP Bread Bags ™) 20x30 cm affixed at the top using three paper clips. There were eight separate bags containing 10 *R. imitans* each. Groups of ten *R. imitans* were added to a peice of filter paper (Watmans ™ no.5) on the inner side of the bag, so that insects could migrate to plants. The settling choices recorded after 24 and 48 hours. To account for those insects that chose to not settle on any plant the proportion of insects on each plant was used as a measure. There were eight replicates of each. Settling choices were recorded when the insects were observed to be present and feeding. It took approximately minutes to assess the positions of all insects.

After the experiment the eight groups of nymphs were split and two nymphs were either placed on an *S. arundinaceus, D. glomerata, H. lanatus* or *A. stolonifera* potted in a plug and placed in a perforated bag as in the prior experiment, each pair only had access to the one plant species. Growth and survivability was to be recorded after this stage, however *R. imitans* nymphs died after less than 48 hours on all plants other than *S. arundinaceus*.

4.2.3 Ordination techniques

Two ordination techniques were used, canonical correspondence analysis (CCA) and principal components analysis (PCA) on field data. In order to visualise differentiation in plant community data PCA was used (Princomp from the *vegan R* package) (Oksanen *et al.*, 2013). Principal components were calcu-

lated by a singular value decomposition of the data matrix (plant abundance rows / sites columns). A biplot was used to visualise the data.

In order to visualise how the insect community related to differences in the plant community CCA was used (from the *vegan R* package) (Oksanen *et al.*, 2013). This function performed an optionally constrained correspondence analysis on the two data matrices (plant community data / sample location, and insect community data / sample location). Visualisation was done using biplots in which the plant data were correlated with the insect data.

4.2.4 Generalised linear models

Using the insect abundance data and percentage plant coverage data from quadrats, Generalised linear models were employed to understand the relationship between the plant communty data and the abundance of different Auchenhorrhyncha species. Using stepwise deletion minimum adequate models were generated (Crawley, 2012). Explanatory variables were the cover of each of the different plants in quadrats and response variables the abundance of each of the different insect species from quadrats. Interactions between explanatory variables were also explored in model building. Poisson error structures with a log link between parameter estimates and the mean of the distribution were used because the response variable were based on count data. In order to visualise interactions in models, the parameter estimates were back transformed from their log values and used to plot a linear model over a scatterplot of percentage plant cover and insect abundance.

4.2.5 Host plant networks

Two types of bipartite networks were compiled. The first used known host plant relationships (Nickel & Remane, 2002) and the Coe Fen plant list,

and was an un-weighted network of host plant associations between insects and their host grasses; number of host plants and number of consumer species. Only grasses were used because the site was principally grass, and the Auchenorrhyncha community was dominated by grass feeders.

A second, weighted, network was compiled using predicted associations of the different Auchenorrhyncha and their host plants based on the abundance of Auchenorrhyncha on the site. This was taken as the total abundance of a given Auchenorrhyncha species multiplied by the proportion of each host plant. For a species which has one host plant it was predicted that all the insects recorded would be associated with that host plant, only. For those that have two host plants the numbers of insects were partitioned between those two host plants relative to their abundance.

For example, if 20 individuals of a insect species that fed on two different plants (a and b) of relative proportional abundances of a = 0.7 and b = 0.1 in the total plant community, the number of individuals were predicted to be distributed between the plants by taking their relative proportions $a = (0.7/0.8) * 20 = 17.5$ and $b = (0.1/0.8) * 20 = 2.5$. Polyphagous species were proportionally and equally divided between all grass plant species.

Network metrics were also calculated including nestedness, the temperature of the matrix (0 means cold, or high nestedness, 100 means hot, a chaotic random network) (Rodríguez-Gironés & Santamaría, 2006). Weighted nestedness a variation of the former that considers interaction frequencies or weights using the method proposed by Galeano *et al.* (2007), ranges vary between 1 (perfect nestedness) and 0 (perfect chaos) the opposite interpretation of non-weighted nestedness. Nestedness scores were compared against 100 null models generated with the same constraints and dimensions as the original models and compared to real scores using t-tests; means were com-

pared because kernel densities were normally distributed. Connectance was calculated as the realised proportion of possible links (Dunne *et al.*, 2002).

Using weighted networks the consequences of removing a host species from a bipartite network was predicted, as a proportion of those Auchenorrhyncha species that would be lost with a reduction in a number of hosts. Using the *second extinct function* with the *bipartite* package, extinction slopes could then be generated to model how a loss of primary producers affects the number of secondary consumers still alive (Memmott *et al.*, 2004; Dormann *et al.*, 2009).

Two R packages were used to carry out these analyses *vegan* (Oksanen *et al.*, 2013) and *bipartite* (Dormann *et al.*, 2009). Nestedness scores, weighted and unweighted, were compared against an appropriate null model, based on 1000 randomisations. The kernel densities of mean average scores for null models were tested against scores from real networks using parametric tests of difference.

4.3 Results

4.3.1 Plant surveys on Coe Fen

The matched plant surveys (Section 4.2.1) demonstrated Coe Fen was clearly dominated by tall fescue *S. arundinaceus*, and although rough meadow grass *Poa trivialis*, was found to have a wider overall distribution on the site, it covered a much smaller total area (Figure 4.3.1). The plant community in this study would be classified under the national Vegetation Classification (NVC) scheme as MG12 *Festuca arundinacea* grassland (*Potentilla-Festucetum arundinaceae*) and the *Lolium perenne-Holcus lanatus* sub-community of MG12.

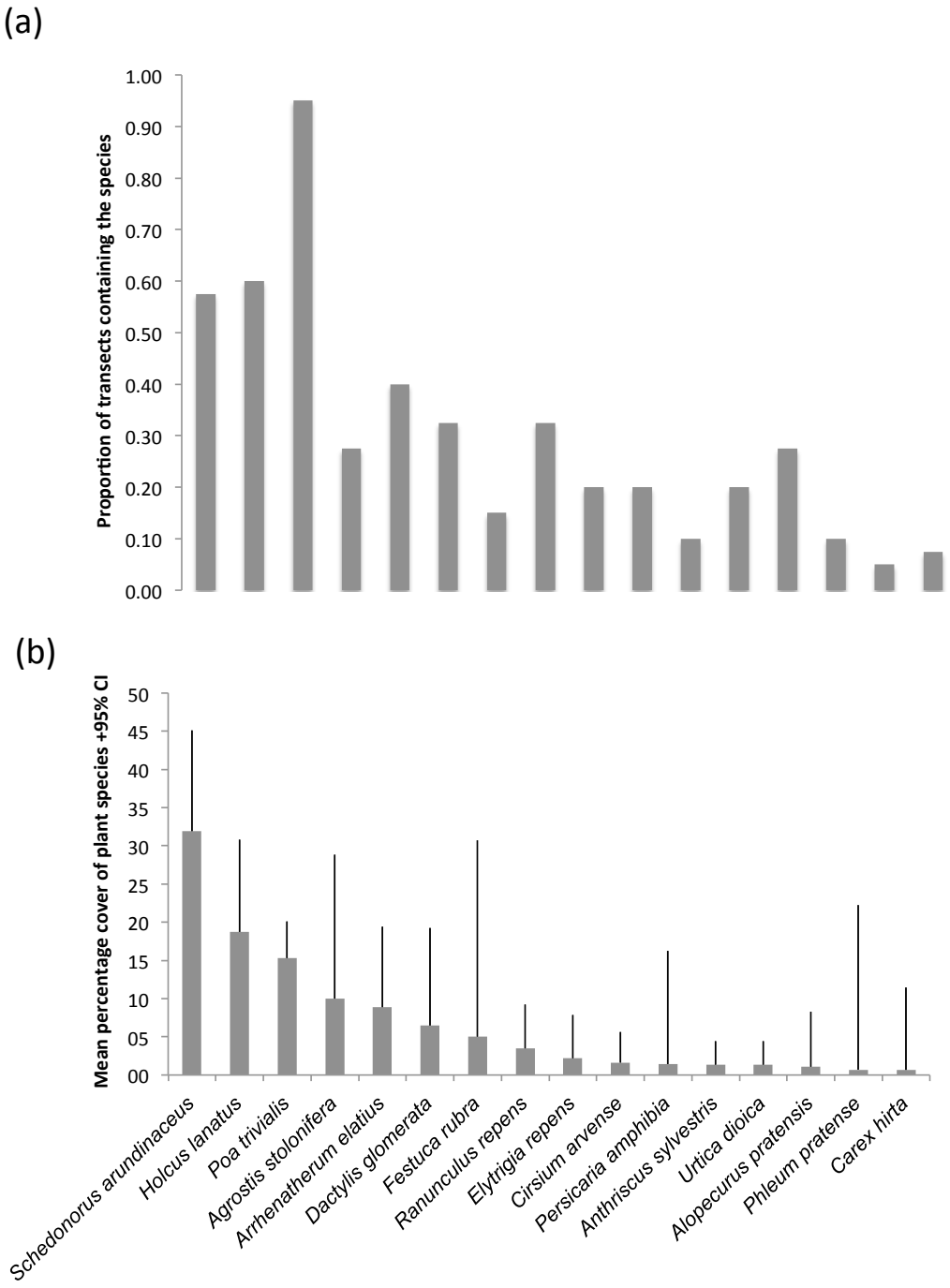

Figure 4.3.1: Summary of different plant species found on Coe Fen. (a) the proportion of the total number of quadrats containing the species and (b) mean cover of each species ± 95 % confidence intervals. Species that occurred in fewer than two quadrats were not included.

Other species were encountered at much lower abundance, typically with a percentage cover of 1% per quadrat and found in no more than two out of all quadrats taken. The remaining species list is:

Amaryllidaceae: wild garlic *Allium vineale* cf
Apiaceae: hemlock *Conium maculatum*
Asteraceae: dandelion *Taraxacum* spp., yarrow *Achillea millefolium*
Caryophyllaceae: mouse–ear chickweed *Cerastium fontanum*
Convolvulaceae: hedge bindweed *Calystegia sepium*, field bindweed *Convolvulus arvensis*
Geraniaceae: cranes–bill *Geranium dissectum*
Malvaceae: mallow *Malva sylvestris*
Poaceae: bushgrass *Calamagrostis epigejos*
Polygonaceae: dock *Rumex conglomeratus*
Rosaceae: creeping cinquefoil *Potentilla reptans*
Rubiaceae: cleavers *Galium aparine*
Fabaceae: white clover *Trifolium repens*

Overall the majority of plants on the site covered less than 1% per species. the community appeared to have a linear rank species abundance relationship, with even proportions of species at the 1% and 10% cut off points (Figure 4.3.2), a typical log-normal relationship. Thirty plant species were recorded, the majority of these grasses (Poacae). There were also dominant dicotyledons present such as creeping buttercup *Ranunculus repens* (Ranunculaceae) and the common nettle *Urtica dioica* (Urticaceae). Nettle generally appeared in patches where it dominated and out-competed grasses where it was encountered.

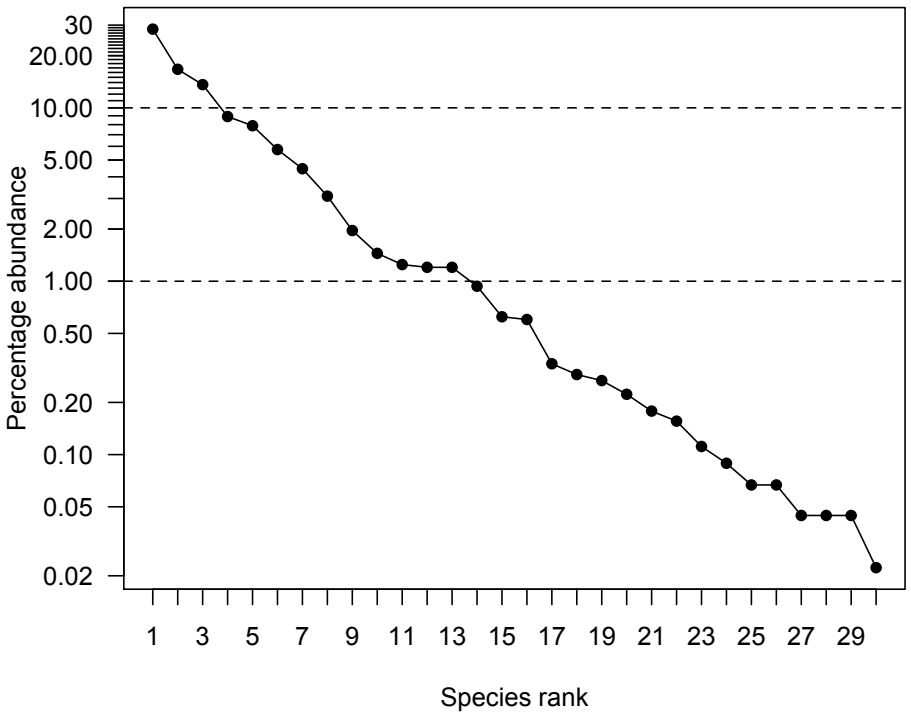

Figure 4.3.2: The percentage abundance of all species represented alongside their ranks. The upper and lower dashed lines represent 1% and 10%

4.3.2 Multivariate analysis of the plant and insect communities

The majority of all plant variables are strongly correlated together, as illustrated by the cluster of plants in the centre of the principal components bi-plot (Figure 4.3.3). The ordination illustrates that only *A. stolonifera*, *H. lanatus* and *S. arundinaceus* are negatively correlated with each other, appearing in separate regions (quarters) from the plot origin, again attributed

to the commonness and dominance of these species within quadrats (Figure 4.3.3). Overall 99% of the variance in the principal components analysis, was explained by the first 10 principal components, the first accounting for 42% of this total variation.

CCA analysis shows a similar story although *S. arundinaceus* appears in the centre of the plot, with the majority of insect species, this is possibly attributed to its dominance in samples. *Macrosteles viridigriseus* appears to be more negatively correlated with other insect species, but positively correlated with *C. arvense* (Figure 4.3.3) which appears to be correlated with other grasses, as does another dicot *T. repens*. Moreover, *Cicadula persimilis* was strongly correlated with *A. millefolium*. *Ribautodelphax imitans* however, was clustered, and therefore positively correlated, with the majority of the rest of the insect community along with its host plant *S. arundinaceus* (Figure 4.3.4). In the CCA analysis 73% of the variability was captured, the first axis accounted for 16% of the total variability in the model, with other axes accounting for a range of between 1% and 16%. However, the distance matrix was not statistically significant ($\chi^2 = 1.30, F_{29} = 0.91, p = 0.67$).

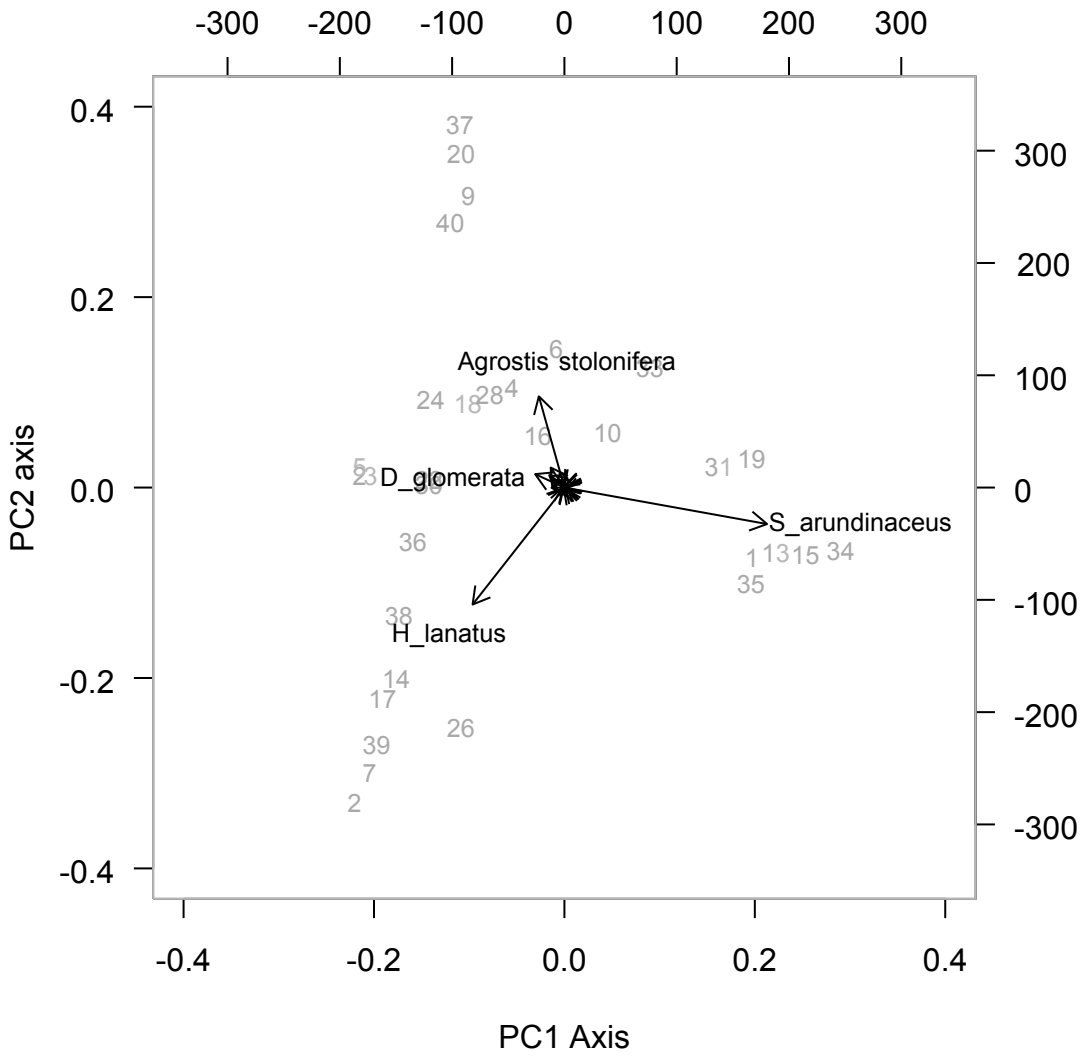

Figure 4.3.3: Principle components analysis plot looking at the plant community data. Arrows show increasing dissimilarity in principal components. Numbers are sites and the plant species as those listed in table 4.3.1 and 4.3.1. The large cluster in the middle of the plot, has the plant names omitted for clarity, and because there are no distinct differences between the communities.

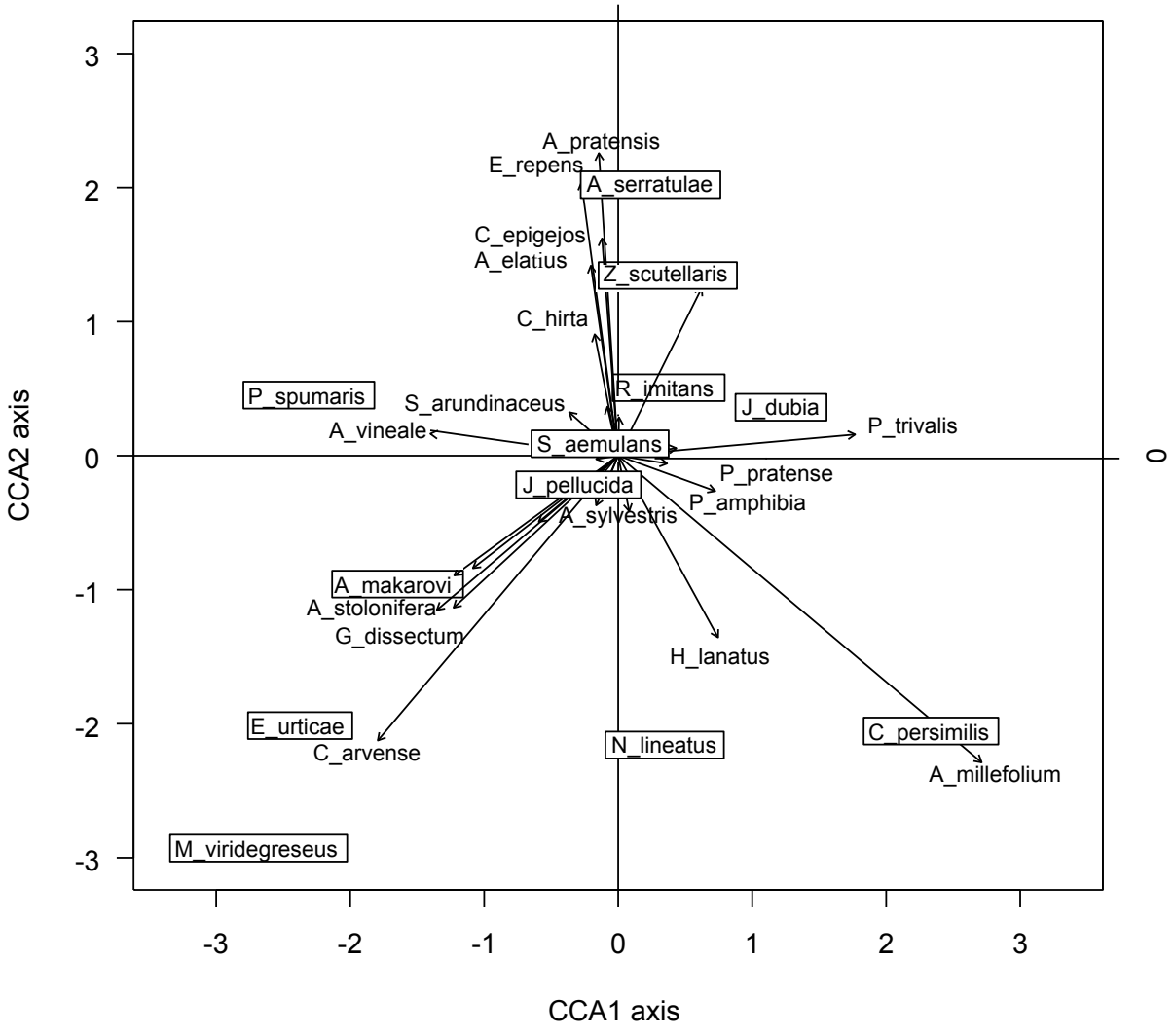

Figure 4.3.4: Canonical–correlation analysis CCA exploring the correlation between the quadrat samples and insect data. Insects appear in boxes, plants without. Arrows show increasing dissimilarity in principal components

4.3.3 Species specific models

Using GLMs there was a clear species-specific preference recorded with four of the species collected in July 2013; the delphacids, *R. imitans* and *J. pellucida*, and the cicadellids, *Zyginidia scutellaris* and *Arthaldeus pascuellus* (Table 4.3.1). *Ribautodelphax imitans* had a significant response to *S. arundinaceus* however, effect sizes were relatively small (Table 4.3.1), effect sizes were also, similarly small for both *J. pellucida* and *Z. scutellaris* (Table 4.3.1). There was a positive interaction between *D. glomerata* and *S. arundinaceus* but, the former plant was not significant outside of this interaction. The effect of increasing *D. glomerata* in interactions, strengthened the relationship of *R. imitans* to *S. arundinaceus* (Table 4.3.5).

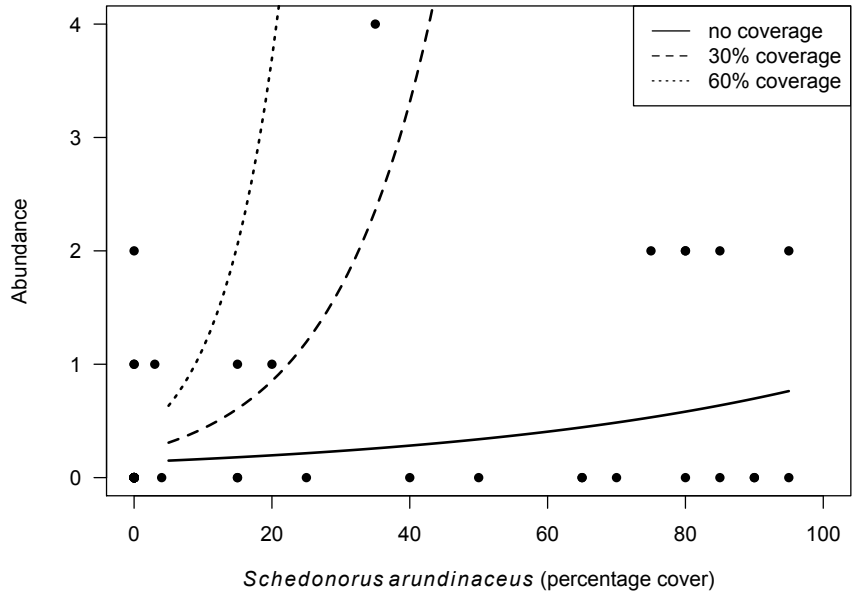

Figure 4.3.5: The relationship between *R. imitans* abundance and the percentage cover of tall fescue. Lines represent the relationship between *R. imitans* and tall fescue at different levels of *D. glomerata*. The lines are from the back transformed parameter estimates in the GLM (Table 4.3.1)

Table 4.3.1: The relationship of plants recorded in quadrats on the abundance of different Auchenorrhyncha species at Coe Fen. Parameter estimates and significance values are given for the model intercept, slopes and interaction terms and the names of each of the Auchenorrhyncha species modelled are abbreviated next to the intercept value. PM is the parameter estimate; *R. im Ribautodelphax imitans*, *J. pel. Javesella pellucida*; *Z. scut. Zyginidia scutellaris*; *A. pasc Arthaldeus pascuellus*. Models use a Poisson error structure and a log link between the parameter estimate and the mean of the distribution. Models have 39 degrees of freedom.

Species	PM	95% CI	SE	t	P
R. im. (Intercept)	-1.988	-3.122, -1.141	0.496	-4.011	< 0.001
S. arundinaceus	0.018	0.003, 0.034	0.008	2.400	0.020
D. glomerata	0.016	-0.033, 0.046	0.018	0.865	0.391
*S. arundinaceus*D. glomerata*	0.002	0.001, 0.003	0.001	2.379	0.021
J. pel. (Intercept)	0.734	0.122, 1.254	0.287	2.553	0.014
S. arundinaceus	0.013	0.005, 0.021	0.004	3.050	0.004
D. glomerata	0.030	0.017, 0.043	0.006	4.677	< 0.001
H. lanatus	0.014	0.004, 0.025	0.005	2.725	0.009
A. stolonifera	0.018	0.006, 0.029	0.006	3.036	0.004
Z. scut. (Intercept)	-1.454	-2.535, -0.613	0.484	-3.006	0.004
S. arundinaceus	0.015	0.002,0.028	0.007	2.207	0.032
P. trivialis	0.032	0.011,0.050	0.010	3.216	0.002
A. elatius	0.023	-0.001, 0.043	0.011	2.095	0.041
D. glomerata	0.023	0.002, 0.041	0.010	2.391	0.021
A. pasc. (Intercept)	-0.890	-1.345, -0.492	0.217	-4.107	< 0.001
D. glomerta	0.023	0.007, 0.037	0.008	3.102	0.003
E. repens	0.054	-0.003, 0.099	0.026	2.114	0.039

4.3.4 Host plant networks

Schenodorus arundinaceus had one of the largest number of herbivore associations (Figure 4.3.6). Nestedness for this network was calculated at 22.86; a relatively 'cold' nestedness temperature, null models were calculated at 22.66 (95% CI = 22.60, 22.73) although significantly different from the actual model ($t_{99} = 6.31, df = 99, p < 0.001$) the effect size was very small, a mean difference of 0.20 (95% CI = 0.14, 0.26), thus suggesting that plants with few monophagous species, also have a large number of generalists. This web has a connectance of 0.56, which is the proportion of possible links in the network calculated as the sum of links divided by the number of cells in the matrix (number of consumers times number of plant species). The average number of links per species, or the number of consumers per host, is 4.67.

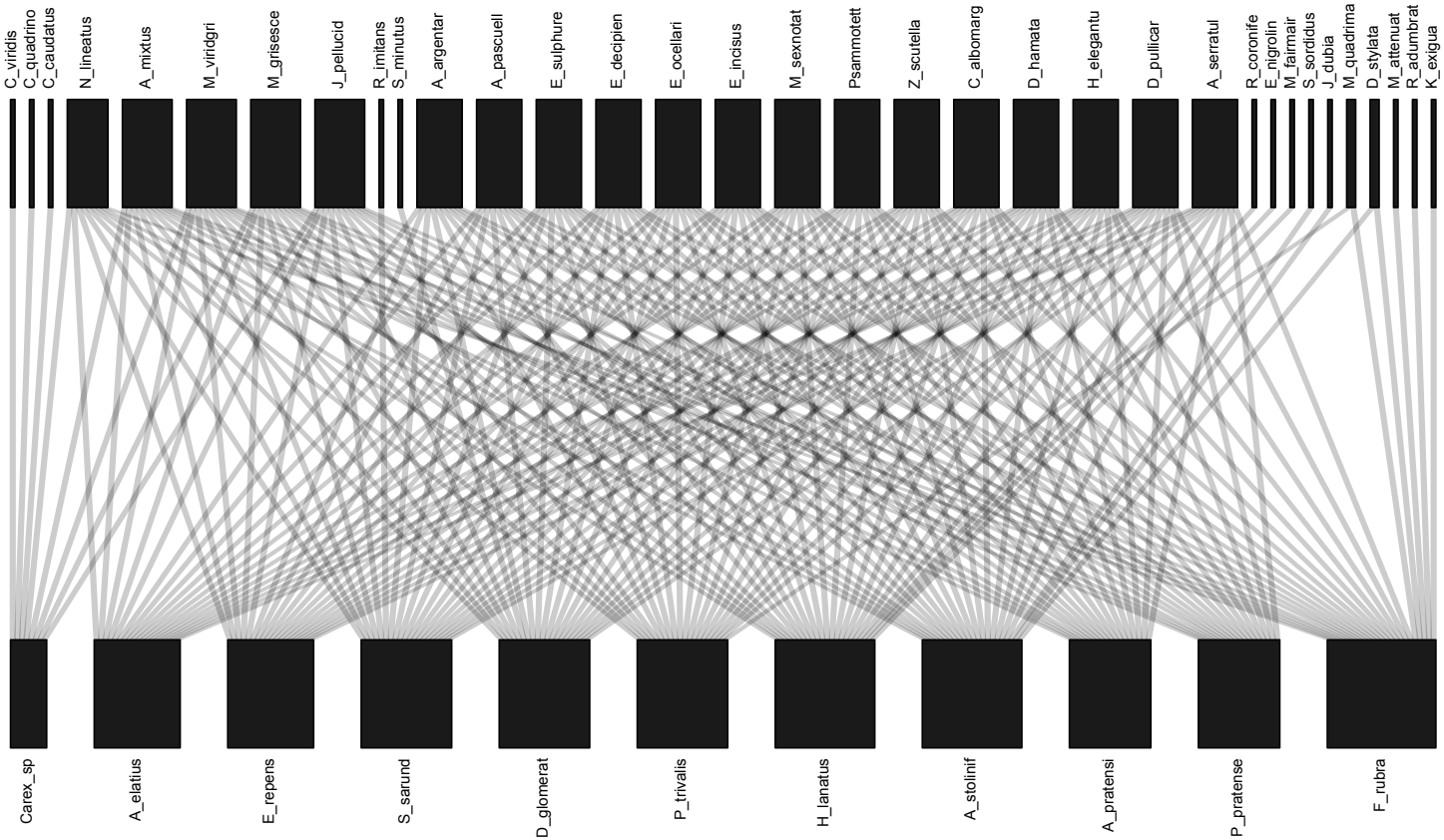

Figure 4.3.6: General un-weighted network of species-species host plant associations for all grass feeding Auchenorrhyncha, using the plant and insect list on Coe Fen. Lines represent interactions and the size of the upper and lower bars indicate relative numbers of either available host plants (overall percentage abundance) or the number of species utilising that host.

The weighted network had a connectance of 0.60, the proportion of possible links in the network calculated as the sum of links divided by the number of cells in the matrix (number of consumers times number of plant species). The average number of links per species is 5.30. Weighted networks had a weighted nestedness of 0.42, significantly greater than null models 0.01 (95%CI = -0.1, 0.02; $t_{99} = 47.86, p < 0.001$) indicative of moderate nestedness within networks (Figure 4.3.7).

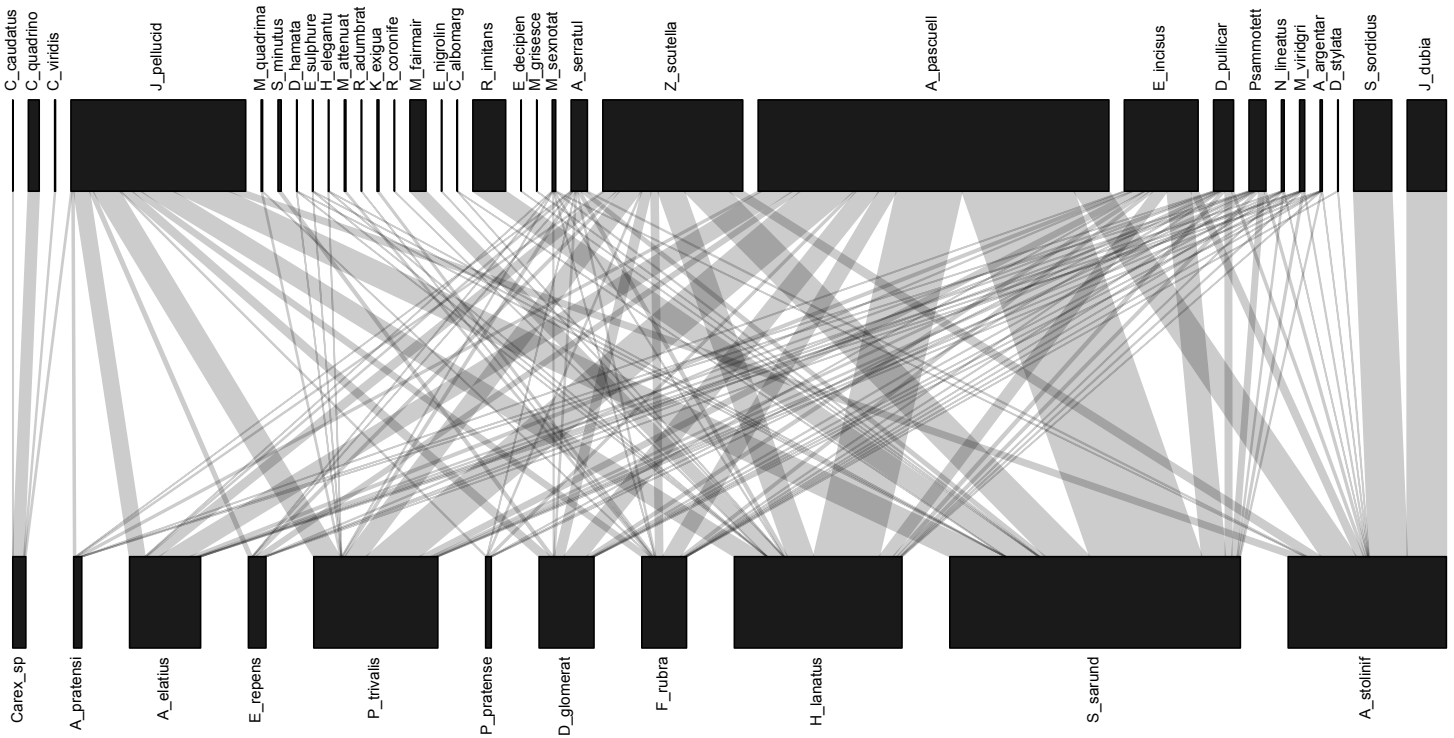

Figure 4.3.7: Weighted network of species-species host plant associations for all grass feeding Auchenorrhyncha, using the plant and insect list on Coe Fen. Lines represent interactions and the size of the upper and lower bars indicate relative numbers of either available host plants or the number of genera utilising that host respectively.

Extinction slopes for the higher trophic level (insects) were calculated at 2.39 with robustness calculated at 0.73, which is the area under the curve generated by the second extinct model (Figure 4.3.8). This value is consistent with a system moderately robust to extinction (0 least 1 most) from loss of primary producers.

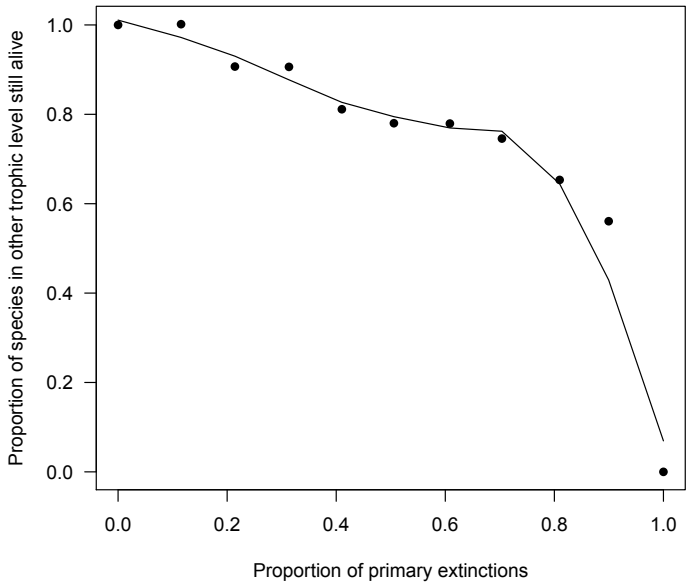

Figure 4.3.8: Extinction risk, modelled as a proportion of those primary producers killed off on the proportion of secondary consumers (Auchenorrhyncha) still alive. The line is added for illustrative purposes, and shows a locally weighted polynomial regression $F_{2,8} = 21.3$, $p < 0.001$, $R^2 = 0.08$.

4.3.5 Extrapolating for the size of the *R. imitans* population on Coe Fen

When the population sizes are extrapolated for the total size of Coe Fen, yearly population estimates for *R. imitans* can be approximated to 5,906

individuals (95% CI = 1,933, 9,880) based on an average of the spring and summer populations over five years, and when the approximate 30% coverage of its host plant is taken into account. Population approximations for *J. pellucida* are markedly higher, although not normally distributed (Median = 293,500, interquartile range = 128,400 – 390,700) (Table 4.3.2).

Table 4.3.2: Approximate adult population sizes for *R. imitans* and *J. pellucida* on Coe Fen, preceded by absolute numbers for each species on a particular sampling date.

R. imitans	Pop. estimate	*J. pellucida*	Pop. estimate	Year	Month
12	7,364	156	319,118	2011	April
11	6,751	156	319,118	2011	July
0	0	11	22,502	2012	July
3	1,841	2	4,091	2013	April
21	12,887	296	605,505	2013	July
9	5,523	80	163,650	2014	April
19	11,660	761	1,556,721	2014	July
2	1,227	131	267,977	2015	April

4.3.6 Laboratory plant choice of *R. imitans*

After the first 24 hours there appeared to be some settling and *R. imitans* was found on other plant species other than its known host, however there was still a substantial majority of *R. imitans* settled on *S. arundinaceus* (Kruskal-Wallis $\chi^2 = 14.6, d.f = 3, p = 0.002$; Figure 4.3.9 a) . After 48 hours, all but one of the *R. imitans* individuals settled on *S. arundinaceus* plants (Kruskal-Wallis $\chi^2 = 22.4, d.f = 3, p < 0.001$; Figure 4.3.9 a).

In addition to these free choice experiments, *R.imitans* were isolated on each of the host plants - following 48 hours on all the alternative plants, the nymphs were all dead which indicated no feeding occurred.

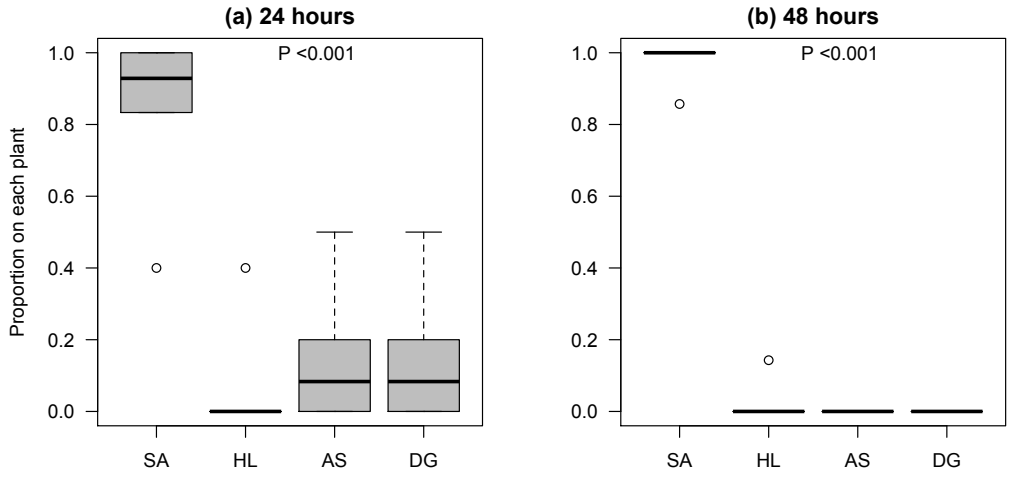

Figure 4.3.9: Host plant choices made by *R. imitans* after (a) 24 hours and (b) 48 hours on different host plants. The codes for the plant types correspond to SA - *Schedonorus arundinaceus*, HL - *Holcus lanatus*, AS - *Agrostis stolonifera* and DG - *Dactylus glomerata*.

4.4 Discussion

4.4.1 Host plant choices and the plant community associated with *R. imitans* and other Auchenorrhyncha

The field and laboratory data demonstrated that *R. imitans* is a specialist, feeding solely on tall fescue in line with the hypothesis. Its host plant is nationally abundant, not just throughout *R. imitans*' range, therefore it is

unlikely that it is a case of a rare host plant distribution fostering guest rarity (Hopkins *et al.*, 2002) (Figure 4.4.1). Moreover, it appears that the study insect species is sharing this plant resource with other members of the community, so their could be other factors that driving its abundance on the site - which will be investigated in subsequent chapters.

The National Vegetation Classification (NVC) is a standard developed for the UK nature conservation agencies (Rodwell *et al.*, 1992; Rodwell, 2006). The NVC aimed to produce a classification and description of British plant communities each named and arranged and with standardised descriptions for each (Rodwell *et al.*, 1992; Rodwell, 2006). Coe Fen indicated MG12, a neutral mesotrophic grassland type typically associated with coastal regions (Rodwell *et al.*, 1992); not a habitat type outlined in the original BAP for *R. imitans*, which stated moderate fidelity to calcareous grassland (JNCC, 2010). However, *R. imitans* may require a very specific set of habitat conditions associated with MG12 mesotrophic grasslands. What these habitat characteristics are is unclear. *Ribautodelphax imitans* has historically been found in coastal calcareous grassland regions , but has more recently been found in managed grasslands inland (Stewart & Bantock, 2015). Calcareous grassland is typically managed for floristic diversity, by low intensity grazing and cutting, with favour given to members of the Fabaceae and other dicotolyedons (Jacquemyn *et al.*, 2003). Potentially a mixed sward with an abundance of dicotolyedons and non-host plant species, such as Coe Fen and others in-land could provide a more suitable habitat.

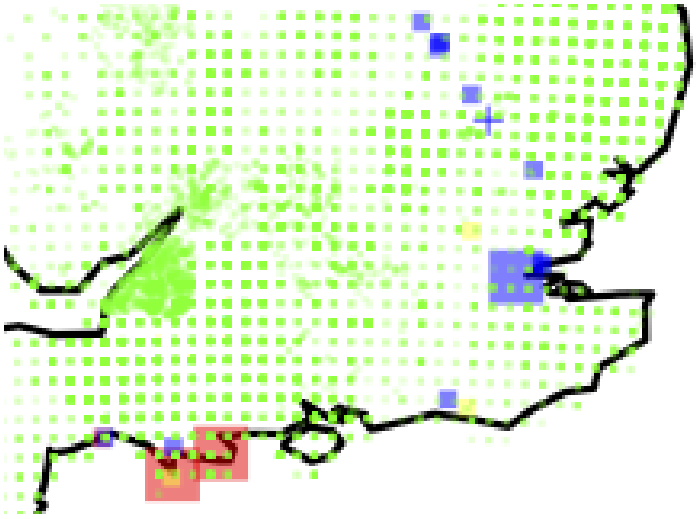

Figure 4.4.1: A map ilustrating the distribution of *R. imitans* overlayed with the distribution data for tall fescue (from the National Biodiversity Network - NBN Gateway www.nbn.org.uk). Green squares represent 10km squares where tall fescue has been observed, the darkness of the square indicates multiple observations. Some of the observations are provided at higher (1km) resolution, where they appear in clusters. The squares are not to scale and are merely representative of data resolution. Other colours plotted are indicative of the year that the data was collected: blue, 2000-present, yellow 1997-2000, and red pre. 1970s. A cross shows Coe Fen.

When considering other species, multivariate analysis showed *M. viridigriseus* appears to be less associated with other insect species, and positively associated with *C. arvense* which is a plant it is not known to feed on (Nickel & Remane, 2002). There were correlations between *C. arvense* and grasses that could account for the relationship between *M. viridigriseus* and this plant. Moreover, *C. persimilis* was strongly correlated with *A. millefolium* a plant this species also does not feed on (Nickel & Remane, 2002). *Ribautodelphax*

imitans however, was positively correlated, with the majority of the rest of the insect community along with its host plant *S. arundinaceus*.

Ribautoldephax imitans in the UK appears to be monophagous on tall fescue, concurring with mainland European data (den Bieman, 1987; Nickel & Remane, 2002). With monophagous insects, advantage is given when their food source is not exploited by others (Cates, 1980, 1981). Tall fescue is not toxic, nor does it have any specialised chemical defences that may put off potential consumers. It is however commonly host to the KY-31 fungal endophyte *Neotyphodium coenophialum*, which is known to have negative effects on insect herbivores, particularly sap sucking Hemiptera (Rudgers & Clay, 2007). Leafhoppers (Cicadellidae) were found to have varying responses to different endophyte strains, indicative of tolerance in some species (Keathley & Potter, 2012). It is possible that *R. imitans* negates the effect of this endophyte, by some underlying physiological mechanism or tolerance. Potentially *R. imitans* in this case is endophyte-adapted, thus gaining it a competitive advantage over other species. Or simply a case of other species being able to tolerate the endophyte to some extent but not cope with it as well as *R. imitans*. Although in this case an adaptive tolerance to one endophyte would not explain the species richness of Auchenorrhyncha associated with this host plant; it was also exploited by a subset of generalist consumers, not simply one specialist in this study.

4.4.2 Implications of host plant associations and networks

Community networks were composed of many links between hosts and consumers, indicating a community composed of generalist consumers alongside a few specialists (Guimarães *et al.*, 2006). Nestedness in host plant networks

indicates smaller assemblages as a subset of larger assemblages (Ulrich *et al.*, 2009). Weighted nestedness scores indicated moderate nestedness within networks, and moderate robustness to extinction from loss of primary producers (Memmott *et al.*, 2004; Burgos *et al.*, 2007). Moreover, the abundance of generalists within the habitat is indicative of 'disturbance specialists' (Andrzejewska, 1962). An unpredictable food supply can be favoured by generalists, that can exploit what is available at the time (Novotnỳ, 1994). This could be related to frequent cutting and disturbance of the site, as is often the case with suburban and urban meadows managed with fixed dates and heavy mowing (Helden & Leather, 2004) and frequently disturbed agricultural lands (Nickel & Hildebrandt, 2003; Eschen *et al.*, 2012; Helden *et al.*, 2015). Frequent disturbance to meadows can lead to a reduction in species richness overall and a disproportionate number of ruderal species (Hildebrandt, 1986; Nickel & Hildebrandt, 2003).

Polyphagous grass-feeding Auchenorrhyncha have been found to select hosts in relation to their nitrogen content, choosing plants that are optimal from a range of potential species (Prestidge & McNeill, 1983). However increased plant diversity is thought to result in greater insect diversity (Maczey, 2005; Novotny *et al.*, 2006; Crutsinger *et al.*, 2006; Helden *et al.*, 2015). In herbivorous communities this can be because of direct as well as indirect relationships. A diverse plant community may have a larger range of specialist consumers when compared to a community composed of just a few plant species (Siemann, 1998; Hopkins *et al.*, 2002). In a specialist community it is therefore more likely that diversity would be driven by a diversity of hosts. However, where generalists are abundant this direct relationship is less apparent. There is generally some degree of relatedness between plant community species richness, nutritional breadth and structural heterogene-

ity; a diverse plant community varies in structure more than one that is less diverse, which could result in greater niche availability for Auchenorrhyncha. It would also provide a greater diversity of nutrient profiles within its host plant community. The underlying mechanism behind how plant communities support biodiversity is not always clear (Kostenko *et al.*, 2012; Humbert *et al.*, 2012), and it is likely it is a combination of microhabitat and host plant relations that maintain community structure (Sanders *et al.*, 2008; Kostenko *et al.*, 2012; Humbert *et al.*, 2012).

The host plant associations of *R. imitans* may be driven by genetic or physiological control, as they are with similar delphacids; for example *Muellerianella* and potentially other *Ribautodelphax* species (Roderick, 1994). Host specificity is important, particularly for rare species or species with low population densities as host fidelity may increase likelihood of contact between sexes (den Bieman, 1987), although this is potentially more likely when the host plant is less common, as the plant species might not be the only factor. Tall fescue is a dominant and common grass, therefore host specificity may not necessarily increase chances of locating mates. However, as a tussock forming grass, tall fescue would form denser sward patches, which could work to increase local density of rare species if preference is shown to these microhabitats (Kruess & Tscharntke, 2002*b*; Dittrich & Helden, 2012; Humbert *et al.*, 2012). Analysis indicated an association between *R. imitans* and *D. glomerata*, as well as with tall fescue. Although experiments ruled this species out as a potential host, it is possible that the growth of this plant species maintains a habitat matrix of tussocks. Both species are highly competitive grasses (Eagles, 1972; Forcella, 1987) and it is possible that these two grasses together help maintain this habitat matrix. This was supported

in models, that showed significant interactions between the two plant species, but no direct relationship between *D. glomerata* and *R. imitans*

The robustness of networks, and the high proportion of generalists in the insect community further supports the idea that it is not so much the direct associations between each of the insects and their hosts that maintains the species richness. Loss of considerable numbers of plants on the site, would not necessarily lead to a rapid decline in the number of Auchenorrhyncha species. Provided the key host plants, such as *S. arundinaceus* are preserved, so will the majority of species richness. Moreover, it is likely that there is no risk to this plant species on the site, owing to both its dominance and invasive nature. However, an over-abundance of this species may raise other ecological issues, leading to host networks unable to support a diverse insect community, because only a finite number of insect species can be supported by a limited number of plants.

4.4.3 Summary

The Coe Fen site is dominated by tall fescue, the host plant of the main study species *R. imitans*. Host plant relationships suggested that although a dominance of this plant on the site is beneficial for *R. imitans*, its persistence is further supported with interactions between it and other plants. It is likely that the relationship between host plants and the Auchenorrhyncha community extend further than a simple case of a greater number of hosts supporting a greater diversity of consumers. It is likley that the ecological characteristics of the host plant, in particular its tendency to form tussocks may be an important factor.

Chapter 5

The role of tall fescue tussocks for Auchenorrhyncha communities and *Ribautodelphax imitans* conservation

5.1 Introduction

Different groups of arthropods respond positively to different swards, some prefer shorter grazed swards while others prefer long or mixed sward types, which are all influenced heavily by management and utilisation (Cherrett, 1964; Mowat, 1974; Dennis *et al.*, 1998, 2001; Kruess & Tscharntke, 2002*b*; Littlewood, Pakeman & Pozsgai, 2012; Littlewood, Stewart & Woodcock, 2012). Previous studies illustrated that natural sward tussocks, a specific growth form (Cherrett, 1964; Luff, 1966; Dennis *et al.*, 1998, 2001) and re-

lated sward structures such as cattle dung islets (Helden *et al.*, 2010; Dittrich & Helden, 2012; Helden & Dittrich, 2016) are ecologically important. This chapter takes this further and looks at how these characteristic sward manifestations maintain biodiversity, and what the implications are for the conservation of *Ribautodelphax imitans* and other Auchenorrhyncha .

Tussocks are thought to be important for arthropods which utilise them as refugia or overwintering habitats (Bayram & Luff, 1993). In more intensively managed grasslands structures such as cattle dung islets. These areas of nutritionally improved tall grass around cattle dung caused by the cessation of grazing and nutritional input from the dung (Helden *et al.*, 2010; Dittrich & Helden, 2012; Helden & Dittrich, 2016), are shown to be a positive force in maintaining biodiversity. They hold a significantly greater proportion of the total biodiversity within fields than grazed areas (Helden *et al.*, 2010). In related studies, differences were found between these structures and the surrounding sward, in the two principal groups of Auchenhorrhyncha, Delphacidae and Cicadellidae, the former preferring fertiliser improved, higher nitrogen, swards (Dittrich & Helden, 2012; Helden & Dittrich, 2016). It is not known as to whether this was an artefact of the sward structure, which was modified by nutrient input (from cattle dung) and therefore considerably more complex structurally than the surrounding sward which was heavily grazed. The system on Coe Fen is very different to more intensively grazed cattle pastures; it is an extensively managed grassland with large numbers of *S. arundinaceus* tussocks, the dominant plant species. (Figure 5.1.1). There may be some similarities in the insect community responses to these tussocks however, and those of cattle sward islets.

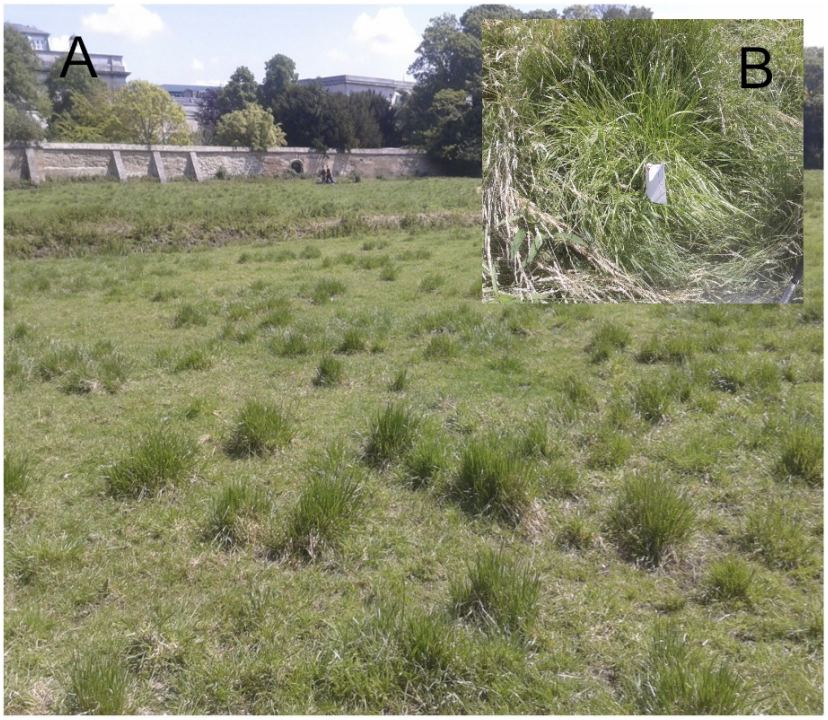

Figure 5.1.1: Tall fescue tussocks on Coe Fen. A the habitat matrix of tussocks B a close up of a tussock used in experimental manipulations

Tall fescue is the host plant of *R. imitans* (Bieman, 1987; Nickel & Remane, 2002; Chapter 2), given this and its tussock-forming nature, it is important to understand more about how the consumer interacts with its host species. *Ribautodelphax imitans* is limited to this host plant, but what are the evolutionary drivers for this? It is not a rare plant, nor is it a toxic plant. Given the benefits of these physiological characteristics and traits, for specialist monophagous species, evolutionary adaptation to hosts could be driven by some other means (Cates, 1981, 1980; den Bieman, 1987). It could be hypothesised that host use is supported by the optimal microhabitat provided by the host plants themselves.

There is a correlation between plant species richness and insect species richness (Sedlacek *et al.*, 1988; Helden *et al.*, 2015). In Auchenorrhyncha It is unlikely that this is solely attributed to links between host plants and consumers, as the communities are often predominantly generalist (Waloff, 1979). However, there is also a strong link between plant species richness and plant structural heterogeneity (Dennis *et al.*, 2001; Huusela-Veistola & Vasarainen, 2000; Vickery *et al.*, 2001; Bell *et al.*, 2002; **?**). Therefore tussocks may have a key role in maintaining structure in a typically homogenous habitat; potentially maintaining a range of microhabitats, and niches, for a diverse range of consumer species (Dennis *et al.*, 2001; Vickery *et al.*, 2001; Bell *et al.*, 2002).

The effect of tussock distribution on grassland species distributions was explored in this chapter. It was hypothesised that arthropods found within tussocks might be affected by pasture sward height within the meadows. Helden *et al.,* (2010) found a beneficial effect of islets, in that a greater proportion of grassland biodiversity was found in these structures compared to outside of them, and this effect increased in shorter swards. Moreover, the structural components of tussocks, such as the length of grass blades and the density of the tussock, might influence how different arthropods respond to them. It was hypothesised that *R. imitans* and other delphacids would prefer more nutrient-rich swards (Dittrich & Helden, 2012), whereas cicadellids would be much less influenced by this, however these preferences would be positively affected by both structure and host plant quality. It was also hypothesised that Delphacidae, in particular *R. imitans*, would prefer higher nutrient inputs than Cicadellidae, with greater proportions found in fertiliser treated tussocks. is is similar to Dittrich and Helden (2012)

who found greater densities of Dephacidae in higher nutrient content, taller swards, however this had not been tested with *R. imitans*.

5.1.1 Aims

1. Investigate if the Auchenhorryncha distributions on the study site are influenced by the presence of tall fescue tussocks throughout the year

2. Understand how the Auchenorrhyncha community responds to tussocks, in particular, to what structural variables do different species respond

3. Investigate how the whole community varies within tussocks, and how this is modified by plant quality

5.2 Methods

5.2.1 Insect collection

Samples of Hemiptera were collected on fifteen occasions between April and October 2011, at approximately two-week intervals (7 21 April; 5 20 May; 2, 14 30 June; 14 27 July; 15 24 August; 9 23 September; 3 18 October). On each date four samples were taken from each section (E1-E5 W1-W5 see general methods section 2.1.2), giving a total of 40 samples per sampling date.

5.2.2 Spatial modeling of plant characteristics and tussock abundance

In January 2012 1m quadrats were placed at 10m intervals north-south and east-west across the whole length of Coe Fen, a total of 175 were taken (fig 5.2.1 in an approximate grid pattern. Within each quadrat the number of tussocks were recorded. The positions of these quadrats were recorded using a differential GPS (Leica GS15). This was used to determine what notational section each quadrat related to (e.g. W1 see general methods chapter section 1.2.1). This enabled the abundance of tussocks to be combined with the sward height and insect abundance data.

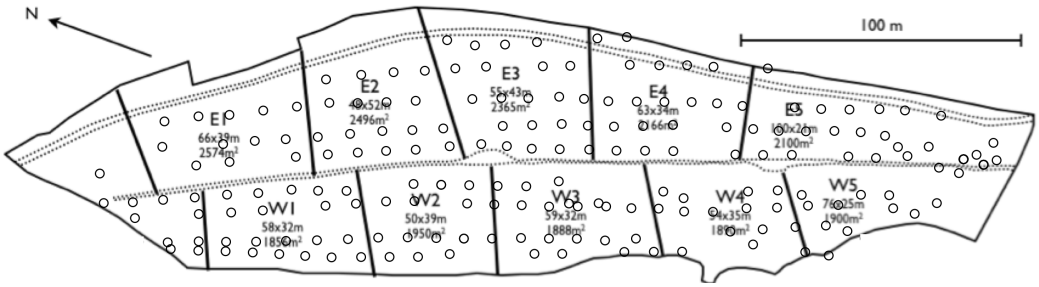

Figure 5.2.1: Position of the quadrats used in determining tussock abundnance on Coe Fen during field work, and their relative positions in relation to the different notional sections used in analysis. The number of quadrats per notional section was for E1-E5 13,17,21,19 and 24 respectively and an W1-W5 20,14,19,15 and 13 respectively.

5.2.3 Experimental manipulation of tussocks

Physical manipulation of tussocks

Tall fescue tussocks were selected for experimental manipulation in section W1 (fig 5.2.1 on the basis of them being well established with a diameter of approximately 30cm each. Initially 24 were selected, however because of interference from cattle the final total sample size was just 12. Of these tussock ($n = 6$) (Figure 5.1.1) were manipulated by cutting at weekly intervals for six weeks (starting 1st May 2013) using standard garden shears to a uniform height of $\approx$ 10cm. An un-manipulated control group was also used ($n = 6$). The manipulations were designed to restrict the overall blade length of the tussocks, and to increase differences between the tussock and the surrounding sward. The surrounding sward was characteristically shorter than the tussocks themselves because of grazing by cattle, grazing of the tussocks themselves was not typically observed. Each tussock was at least 2m apart from the next in the study.

To collect insects a Vortis suction sampler was placed over the tussock, and three subsamples were taken from the interior tussock area (the 30cm diameter area within a tussock), and the tussock rim (the immediate edge of a tussock taken from outside the 30cm internal area) (Figure 5.2.2) for each tussock. Each sample consisted of a 16 second suck on full power, in quick succession to minimise loss of insects through disturbance. The diameter of the collecting area of suction sampler was 0.2 m^2. Insects were then transferred directly into 70% ethanol solution in the field.

Measurements of grass followed insect collection in either the tussock rim (Figure 5.2.2 B i) or the tussock interior (Figure 5.2.2 B ii). Two measurements were taken. Firstly **sward length**: 10 random grass blades were

selected, and measured from soil level to the tip of the grass blade using a standard 1m ruler (measurements to the nearest 5mm). Secondly **sward height**: measurements were taken using a Jenquip Filips Folding Plate Pasture Meter (Anon, 2016*b*) [otherwise known as a drop disk] to the nearest 5mm on either the tussock interior or tussock rim (figure 5.2.2B). Ten measurements were taken for each tussock, and in data analysis the mean values were used, as measurements conformed to normality.

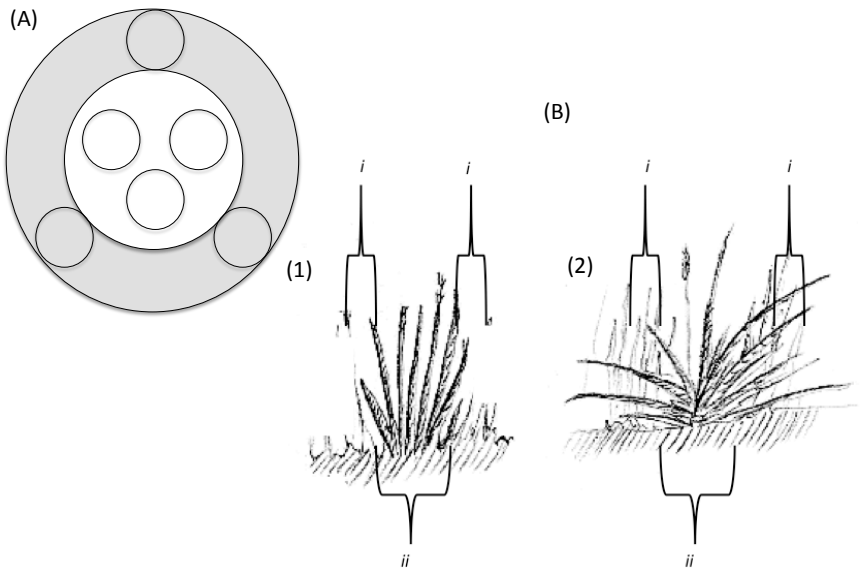

Figure 5.2.2: (A) the sampling regime of a tussock showing the positions of the sucction sampler as small circles, a large white circle as the inner tussock area and the grey area as the tussock rim area (B) Illustration of two tussocks (1) short blade length tussock (2) a long blade length tussock, where the blades lay flatter on the surface of the tussock. (i) tussock rim area (ii) tussock interior

A drop disk was used alongside the ruler measurement of blade length because they provide different, but informative, measures of sward structure. Grass can lie at different angles across the pasture or meadow (Figure 5.2.2 B), therefore measurements with a drop disk may not be representative of individual blade length; only the vertical height from substrate. These measurements are affected by phytomass or pasture density, the drop disk tending to fall lower in less dense swards (Sharrow 1984). All data were tested for normality using a Shapiro-Wilk test, so that the appropriate central tendency was used.

5.2.4 Manipulation of tussocks with fertiliser

Naturally occurring tall fescue tussocks were treated using fertiliser (Westland, Growmore fertiliser: NPK 7-7-7, solid granulated fertiliser) which was watered in along with a control of untreated water in summer 2014. For every fertiliser application a fixed quantity of one litre of water was used. Two different fertiliser applications were used alongside a control fallow tussock (no fertiliser added), and non tussock (extra-tussock) sward.

A total of 20 tall fescue tussocks were given a 30g fertiliser application (as per the recommendation for the brand) on the 30th of April and 20 further tussocks were left fallow (control). Of the fertiliser treated tussocks, six were disturbed by cattle so the 14 remaining fertiliser treated tussocks received an additional fertiliser treatment on the 30th of May. Another 20 untreated tussocks then received a fresh dose of 30g fertiliser on 30th May. These became the high and standard fertiliser treatments respectively. Treatments were distanced at least 3m apart to avoid leaching effects from fertiliser treatments. Tussocks were labelled with 50cm bamboo canes. At the end of experiments there were seven high fertiliser replicates, six standard fertiliser

replicates and six unimproved (fallow) replicates remaining, six non tussock (Extra-tussock) sward samples were also taken as a control.

Insects were collected using a Vortis suction sampler on 16th July 2014, each sample consisted of three 16 second sucks in the tussock interior (Figure 5.2.2), each sample was then transferred directly into 70% ethanol solution in the field. Sward height measurements in this experiment were made with the drop disk to the nearest 5mm.

5.2.5 Statistical methods

Habitat model selection

All the environmental characters that were gathered were used to build generalised linear models (GLMs) predicting the following response variables:

- Total abundance of Auchenorrhyncha
- Total number of Auchenorrhyncha species
- Presence or absence of *R. imitans* in the sample
- The abundance of *R. imitans*
- The abundance *Javesella pellucida*
- The abundance of Delphacidae
- The abundance of Cicadellidae

Models were selected using stepwise deletion process from which the maximum model including all variables and their interaction terms was reduced down to a minimum adequate model, in which all variables were significant. The variables included in the initial model were:

- Sward height
- Number of tussocks in each section of Coe Fen (see general methods)
- The sampling date (days from start of year)

In the case of the presence absence models, a 0 was assigned where there were no individuals in a sample and a 1 where there were. This new response parameter was used in logistic GLM models, with a binomial error structure and a logit link ($log\frac{p}{1-p}$) between the parameter and the mean of the distribution. Count based models used a GLM with a Poisson error and a log link between the parameter estimate and the mean of the distribution.

Minimum adequate models that predicted abundance of Auchenorrhyncha and their relationship with tussocks were selected from the maximum model:

$$\hat{y} \approx d + d^2 + sh + (tc) + ta + [sh * ta]$$

$\hat{y}$ is the response variable predicted by $d + d^2$ the unimodal effect of sampling date, sh sward height, tc the total catch (not used in abundance models), ta tussock abundance within the section, and $[sh * ta]$ the sward height tussock abundance interaction.

In order to elucidate the responses of insects to habitat variables within tussocks, GLMs were used. Minimum adequate models were selected from the following full model:

$$\bar{y} \approx tish + trsh + tisl + trsl + tish * trsh + tisl * trsl + M + loc + (1|ID)$$

Where $tish$ was tussock interior sward height, $trsh$ tussock rim sward height (the drop disk measurements within and outside of tussocks), $tisl$ tussock interior sward length, and $trsl$ tussock rim sward length; the average blade length (taken from 10 blades of grass). Whether the tussock was un-manipulated or manipulated by cutting M, was also included in the maximum model (as a presence absence measure. loc the location that the samples were taken from was included, as were random effects $1|ID$t, the identity of each individual tussock. The random effects account for any nestedness, independent variables may not be independent of each other if they are taken from the same tussock. Interaction terms were also included were $tish * trshtisl * trsl$ as the interaction between tussock interior sward height and tussock rim sward height and tussock interior sward length and tussock interior sward length respectively.

GLMs that explored the proportion of individuals within a tussock, comparing the number in tussock rims ne to those in the tussock interior ni. Models were selected from the maximum model. These models used a binomial error structure with a logit link function:

$$\frac{ni}{ne + ni} = \bar{y} \approx tish + trsh + tisl + trsl + tish * trsh + tisl * trsl + M$$

Interpretation of generalised linear models

Parameter estimates from GLMs were plotted to aid in interpretation of models with multiple parameter values. The *predict R* function was used R, in order to back transform parameter estimates into continuous variables that could be plotted. When there were multiple explanatory variables in models 25, 50 and 75% quartiles were were plotted as separate lines. Median values and quantile ranges were used in this case because some parameters did not conform to normality. Models were plotted as:

$$Y = m\hat{x}_1 * x + m\hat{x}_2 * x + m(Q_1|Q_2|Q_3) * x + c$$

Where $m\hat{x}$ is median average slope for a given parameter estimate (subscript numbers denote different parameter coefficients), $m(Q_1|Q_2|Q_3)$ is a fixed extreme value for a parameter, for example the 25, 50, or 75% quantile for variables (e.g. tussock abundance), x the continuous variable (e.g sward height) and c the intercept. In the case of logistic models, the logit parameter estimates were back transformed using antilogit.

Multivariate analysis

The community structure recorded from each treatment was assessed using non-metric multidimensional scaling (NMDS). Treatments were compared to insect communities using the *metaMDS* function in the R *vegan* library, which transformed the data with a Wisconsin double standardisation and square root transformation (Oksanen *et al.*, 2013). The *Adonis* function was

used to fit linear models to the distance matrices by using a permutation test with pseudo F-ratios to test for significance in the NMDS (Oksanen *et al.*, 2013).

5.3 Results

5.3.1 Survey results

Out of the 10 plots surveyed numbers of tussocks encountered ranged from 1 to 42, with a Median of 17 (n =1, 2, 6, 9, 12, 22, 22, 23, 33 & 42). When plots were divided into those that had high numbers of tussocks (> 12 recorded in random sampling) and those that were not (low numbers of tussocks ≤ 12), it became apparent that in shorter swards ($\leq 9.4cm$) the higher abundance of tussocks maintained both abundance and species richness of Auchenorryncha (Figure 5.3.1).

There were significant differences in the abundance of individuals in tussock abundant (**high**) plots compared to those that were not (**low**), in short swards ($W = 19,472, P < 0.001$) but not long ($W = 66,43, P = 0.4796$) (Figure 5.3.1). There was also significantly higher species richness in tussock dominated plots compared to those that were not, in short swards ($W = 18,534, P = 0.001$) but not long ($W = 6,643, P = 0.480$) (Figure 5.3.1)

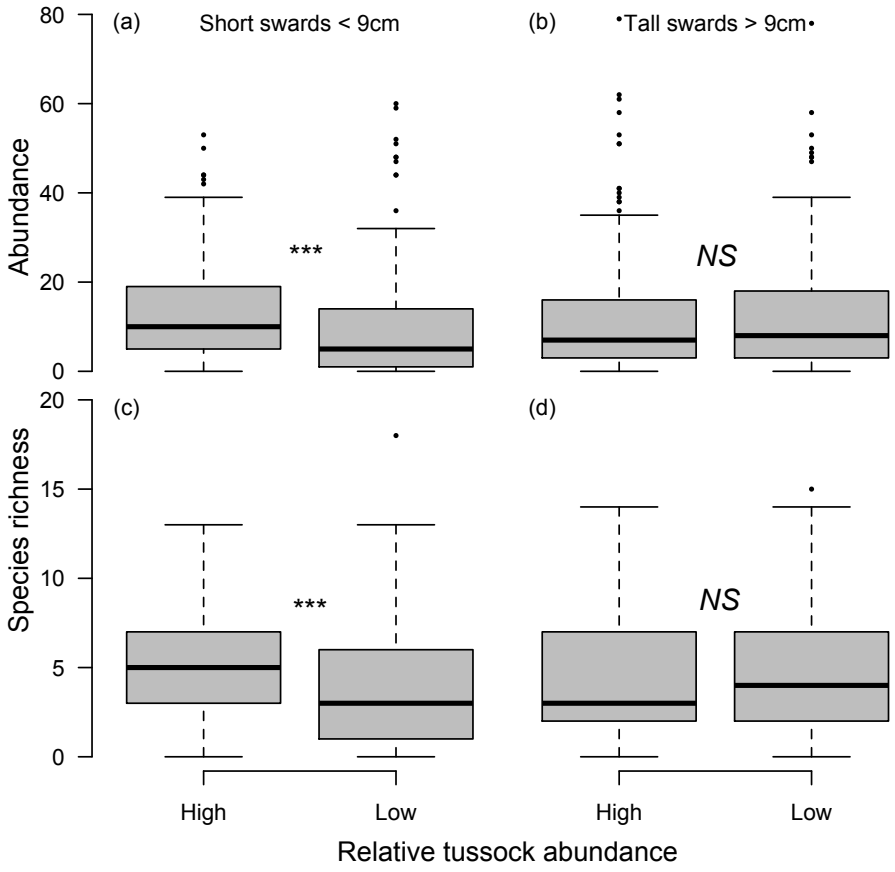

Figure 5.3.1: The difference in Auchenorrhyncha abundance and species richness, between short (a & c) and long (b & d) sward types. Swards were classified as short when they had a height recorded by the drop disk of less than 9.4cm, and as long when greater than 9.4cm. High were those that were abundant in tussocks (> 12 recorded in random sampling $n = 5$) and Low those that were not (≤ 12,) $n = 5$). *** denotes significance at the < 0.001 level

The models predicted that the abundance of Auchenorrhyncha was influenced by date, explained by the unimodal affect of time, tussock abundance, and sward height. When sward height and tussock abundance interacted within the model a pattern emerged in which the tussock abundance had a negative effect on the positive sward height effects; or to paraphrase increasing the abundance of tussocks reduced the positive effect of sward height (Table 5.3.1). The species richness models showed the same patterns. However in these models abundance was included, because of associations between the number of individuals encountered and likelihood of encountering more species. Sward height appeared to have a stronger influence on the number of species likely to be encountered when compared to the total abundance models, whereas tussocks had a less positive influence. The interaction between the two, although it shows the same direction of relationship, it is weaker, with parameter values of log_e 0.003 (95% CI = -0.004,-0.002) versus log_e -0.001 (95% CI = -0.002,0.00) (Table 5.3.1).

The binomial model that looked at the presence and absence of *R. imitans* used the same model composition as above (Table 5.3.1 c). In this model, when sward height and tussock abundance interact the same pattern emerged. Increasing sward height and tussock abundance increased the probability of encountering *R. imitans* with tussocks reducing the negative effect of shorter swards (Figure 5.3.2).

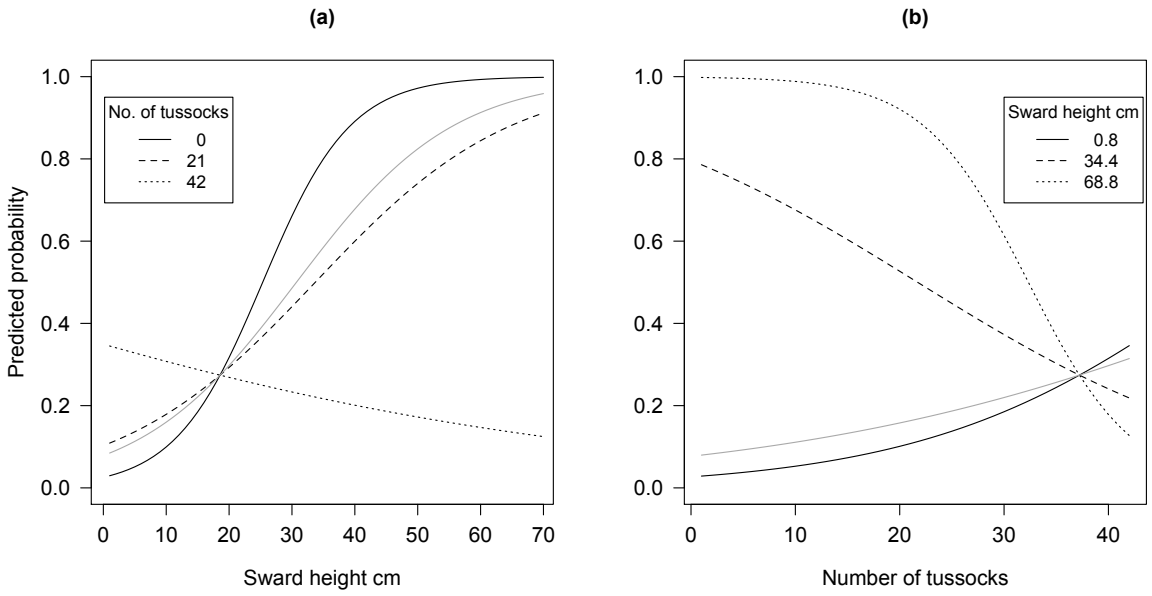

Figure 5.3.2: The effect of increasing tussock abundance (a) or sward height (b) on predicting presence or absence of *R. imitans*. The predicted probability, is the inverse of the logit link: $log\left(\frac{p}{1-p}\right)$ or the approximate likelihood of encountering *R. imitans*. The lines of the graph either represent different extremes of measurement (a) sward height, (b) number of tussocks. The solid grey line represents the median values of 8.3 cms sward height, or 17 tussocks.

Table 5.3.1: Generalised linear models for number of species (a) total abundance (b) and (c) presence absence model of *R. imitans*. Count based models use a quasipoisson error structure because of over dispersion - no AIC reported in this case, and a log link between the parameter estimate and the mean of the distribution. d sampling date, sh sward height, tc the total catch (not used in abundance model), ta number of tussocks within a plot, and $[sh * ta]$ the sward height tussock abundance interaction. The presence absence models use a binomial error structure and a logit link; $log\left(\frac{p}{1-p}\right)$, between the parameter estimate and the mean of the distribution. All models have 599 degrees of freedom

Coefficient	Estimate	95% CI	S.E	z or t	p
(a) number of species				t	
(Intercept)	-0.833	-1.134, -0.532	0.154	-5.418	< 0.001
d	0.372	0.321, 0.423	0.026	14.337	< 0.001
d^2	-0.020	-0.022, -0.017	0.001	-14.122	< 0.001
ta	0.007	0.001, 0.013	0.003	2.336	0.020
sh	0.037	0.017, 0.058	0.010	3.651	< 0.001
tc	0.018	0.015, 0.021	0.001	13.747	< 0.001
ta * sh	-0.001	-0.001, 0.000	0.000	-3.079	0.002

Continued...

Coefficient	Estimate	95% CI	S.E	z or t	p
(b) total abundance				t	
(Intercept)	-1.613	-2.209, -1.017	0.304	-5.304	< 0.001
d	0.735	0.638, 0.832	0.049	14.903	< 0.001
d^2	-0.036	-0.041, -0.031	0.003	-13.895	< 0.001
ta	0.020	0.010, 0.031	0.005	3.858	< 0.001
sh	0.111	0.077, 0.145	0.017	6.421	< 0.001
ta * sh	-0.003	-0.004, -0.002	0.000	-5.339	< 0.001
(c) presence or absence of *R. imitans*: AIC = 393.87				z	
(Intercept)	-5.842	-7.897, -3.965	1.00	-5.839	< 0.001
d	0.607	0.276, 0.972	0.177	3.436	0.001
d^2	-0.05	-0.073, -0.029	0.011	-4.379	< 0.001
sh	0.148	0.020, 0.274	0.064	2.294	0.022
ta	0.074	0.034, 0.117	0.021	3.535	< 0.001
tc	0.064	0.044, 0.086	0.011	5.912	< 0.001
ta * sh	-0.004	-0.008, -0.001	0.002	-2.269	0.023

5.3.2 Physically manipulated tussocks

There was no difference in sward heights measured with the pasture meter between interiors and rims, nor was this affected by manipulation status (Manipulated: paired t-test, $t_5 = 0.079, p = 0.941$. Non-manipulated paired t-test, $t_5 = 0.048, p = 0.963$). Mean sward heights on the tussock rims were estimated at 31.74 cm (95% CI = 27.71, 35.78) and tussock interiors 31.49 cm (95% CI = 27.05, 35.92) (Figure 5.3.3 a).

Sward length however was affected by physical manipulation. Tussock rims had significantly longer blades than tussock interiors (Paired t-test:

$t_{11} = -5.544, p < 0.001$). The mean sward length of manipulated tussock interiors was estimated at 28.37 cm and non-manipulated 41.46 cm a mean difference of 13.09 cm (95% CI = 23.0, 31.6; $t_{11} = -2.8818, p = 0.014$). Sward lengths were significantly greater on tussock rims compared to tussock interiors; whether manipulated through cutting (paired t-test: $t_5 = -6.0789, P = 0.002$; mean difference = 23.4, 95% CI = 33.3, 13.5) or not (Paired t-test: $t_5 = -2.6975, p = 0.043$; mean difference = 16.4 cm, 95% CI = 32.1, 7.7). The sward length of tussock rims was unaffected by manipulation status ($t_1 1 = 1.2147, p = 0.254$) (Figure 5.3.3 b).

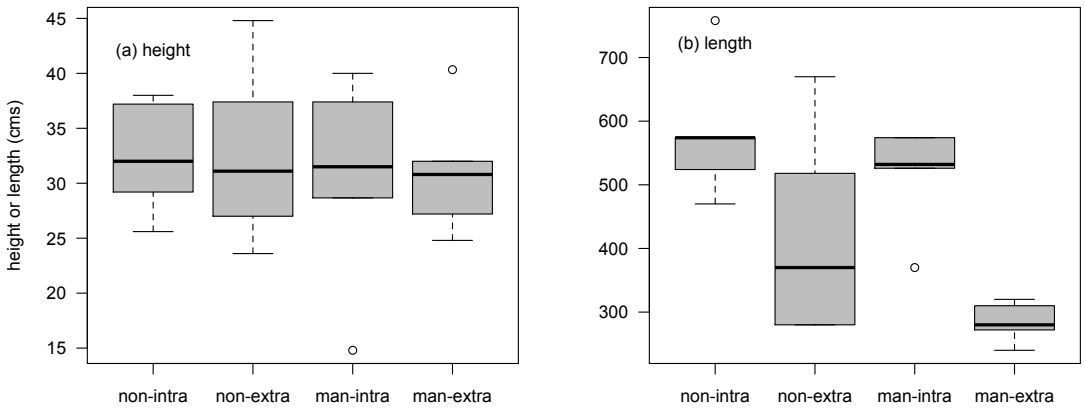

Figure 5.3.3: The effect of manipulation status on the sward heights of tussock rims and interiors (a) and the sward lengths of tussock rims and interiors (b)

There was no significant difference in the abundance of Auchenorrhyncha in the tussock interior compared to the tussock rim (Paired Wilcox test:$V = 57, P = 0.168$). Cicadellids showed no statistically significant differences (Paired Wilcox test:$V = 18, P = 0.189$) but a very small numerical difference, delphacids were also not significantly different (Paired Wilcox test: $V =$

57.5, $P = 0.157$). However, results could indicate a skew towards interiors for cicadellids and rims for delphacids (Figure 5.3.4).

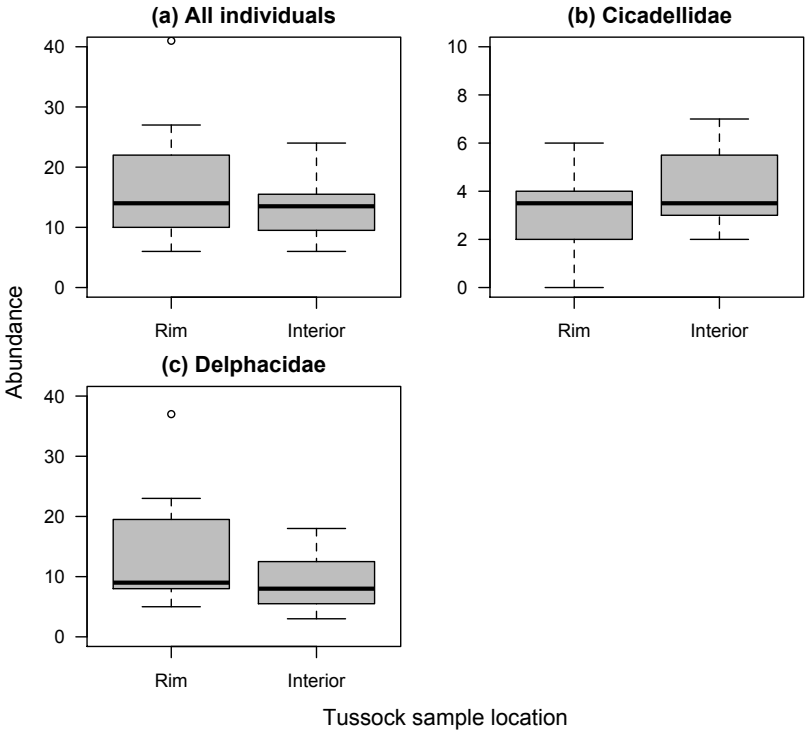

Figure 5.3.4: Comparison between the total catch of Auchenorrhyncha (a) cicadellids (b) and delphacids (c) in the tussock interior and rim swards.

GLMs demonstrated that there was a significant effect of sward height on Auchenorrhyncha and delphacid abundance. Sampling location affected responses, with greater abundance found on the tussock rim (Table 5.3.2 a b; Figure 5.3.4). Cicadellids however showed a different pattern; they responded to the parameter, tussock sward length, but the parameter values indicate a significant small effect, log_e 0.004 (95% CI = 0.001, 0.006; Table 5.3.2 c). The two measures of length and height were interrelated ($F_{1,20} = 5.803, P = 0.025, R^2 = 0.17$); however, the responses to one but

not the other, suggest independent responses for either group Delphacidae and Cicadellidae. Models for *R. imitans* and species richness could not be constructed because the numbers were too small for reliable models to be selected. However, a significant species specific model could be constructed for *J. pellucida* which showed both positive responses to both tussock exterior sward height with a greater abundance on the tussock rims (Table 5.3.2).

Table 5.3.2: Minimum adequate generalised linear models, comparing different coefficients on the given response variables (a) All Auchenhorryncha (b) Delphacidae (c) Cicadellidae (d) *Javesella pellucida*. *tish* was tussock interior sward height, *trsh* tussock rim sward height, *tisl* tussock interior sward length, *trsl* tussock rim sward length, *loc* was the location of the sample; the tussock rim in this case was measured on the intercept (i.e positive values indicate more on rims than interiors and visa versa). All models use a log link and a Poisson error structure.

	Estimate	95% CI	Std. Error	z value	p
(a) All Auchenhorryncha	AIC = 143.3				
(Intercept)	1.188	0.483, 1.894	0.360	3.300	0.001
loc	0.157	0.043, 0.272	0.059	2.689	0.007
tish	0.004	0.002, 0.006	0.001	4.016	<0.001
(b) Delphacidae	AIC = 145.3				
(Intercept)	-0.145	-1.155, 0.866	0.515	-0.28	0.779
loc	0.261	0.127, 0.394	0.068	3.822	<0.001
trsh	0.002	0.000, 0.005	0.001	1.999	0.046
tish	0.005	0.003, 0.007	0.001	4.997	<0.001
(c) Cicadellidae	AIC = 85.9				
(Intercept)	-0.848	-2.293, 0.598	0.738	-1.149	0.251
trsl	0.004	0.001, 0.006	0.001	2.925	0.003
(d) *Javesella pellucida*	AIC = 143.0				
(Intercept)	1.188	-1.244, 0.777	0.36	3.3	0.001
loc	0.157	0.138, 0.411	0.059	2.689	0.007
tish	0.004	0.00, 0.005	0.001	4.016	<0.001

The proportion of all individuals within tussock interiors were negatively affected by tussock interior sward lengths log_e -0.003 (95% CI = -0.004, 0.001) (Table 5.3.3). Delphacids were also negatively correlated with sward length, the proportion within tussock interiors decreasing with this measure log_e -0.003 (95% CI = -0.005, -0.001) (Table 5.3.3); however, this relationship although significant, was not strong (Figure 5.3.5). Models could not be constructed for cicadellids as no parameter values were significant.

Table 5.3.3: Minimum adequate generalised linear models, comparing different coefficients on the response variables. (a) All Auchenorrhyncha (b) Delphacidae. *trsh* = tussock rim sward height, and *tish* = tussock interior sward height. Models have 11 degrees of freedom. Models use a logit link $log\left(\frac{p}{1-p}\right)$ and binomial error structure

Coefficient	Estimate	95% CI	SE	z	p
(a) All Auchenorrhyncha	AIC = 66.5				
(Intercept)	-0.718	-1.852, 0.415	0.578	-1.242	0.214
trsh	0.042	0.005, 0.079	0.019	2.241	0.025
tisl	-0.003	-0.004, -0.001	0.001	-3.282	0.001
(b) Delphacidae	AIC = 64.0				
(Intercept)	0.689	-0.027, 1.405	0.365	1.885	0.059
tisl	-0.003	-0.005, -0.001	0.001	-3.176	0.001

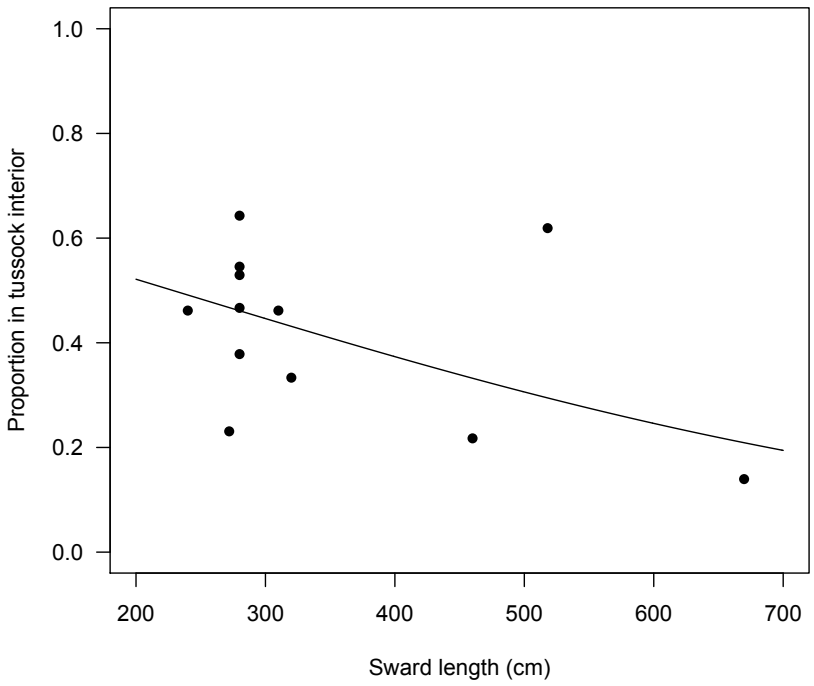

Figure 5.3.5: Relationship between the sward length of tussock interiors and the proportion of delphacids found in the tussock interior compared to the rim. Line was from binomial GLM in table 5.3.3 and shows predicted probability of delphacid presence.

5.3.3 Fertiliser manipulated tussocks

Those treatments with highest fertiliser applications had the highest growth increase (Figure 5.3.6 a; Table 5.3.4 a). The greatest abundance of Delphacids were found in the tallest, and those fertilised tussocks which received the greatest amount of fertiliser (Figure 5.3.6 c; Table 5.3.4 d), whereas cicadellids appeared to prefer non-tussock areas (Extra-tussock) (Figure 5.3.6 d; Table 5.3.4 c). In addition there was considerable overlap in species rich-

ness recorded with all treatments, a maximum mean value of 10 species (Figure 5.3.6 d). GLMs did not include the variable sward height because it was non significant in model selection (Table 5.3.4).

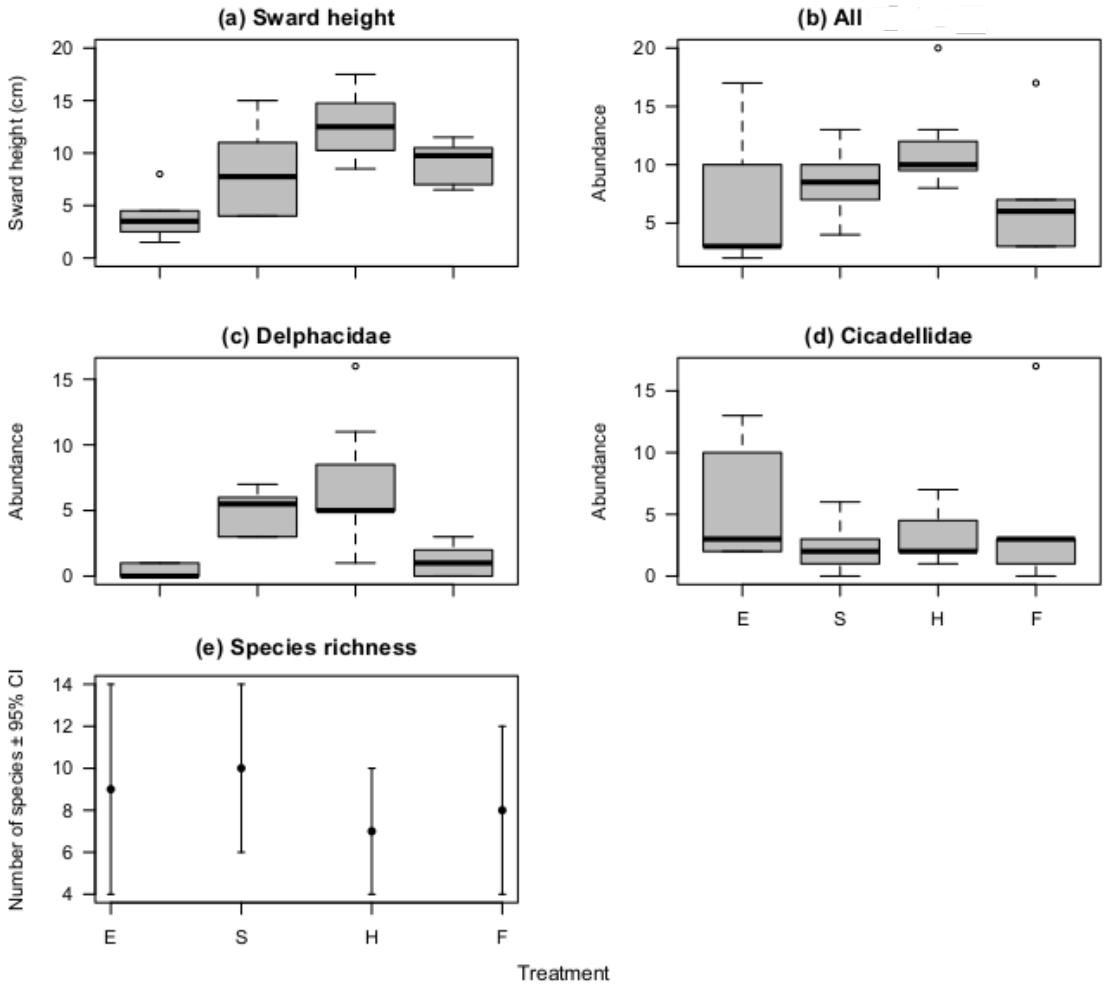

Figure 5.3.6: The effect of different treatments E – extra-tussock (the area outside of a tussock); S – single application of fertiliser; H – high fertiliser application; F – fallow tussocks, on (a) sward height (b) abundance of all Auchenorrhyncha (c) abundance of Delphacidae (d) abundance of Cicadellidae (e) Auchenorrhyncha species richness, these are presented as error plots because the species richness ± 95% CI was calculated using the jacknife method (as per chapter 3).

Table 5.3.4: Generalised linear model outputs showing how different parameters (a) sward height (b) total abundance (c) Cicadellidae and (d) Delphacidae, respond to different treatments. All model parameter values are from GLMs with a Poisson error structure and a log link between the parameter estimate and the mean of the distribution. The intercept is modelled as the extra-tussock, and so can be treated as a control to compare to the other three treatments. Models have 22 degrees of freedom

	Parameter	95% CI	SE	z	p
(a) Sward height	AIC = Inf.				
(Intercept) extra-tussock	1.365	0.932, 1.744	0.206	6.618	< 0.001
Standard	0.745	0.266, 1.252	0.251	2.974	0.003
High	1.170	0.740, 1.643	0.229	5.110	< 0.001
Fallow	0.850	0.381, 1.352	0.246	3.450	0.001
(b) Total abundance	AIC = 95.87				
(Intercept) extra-tussock	-0.223	-1.393, 0.620	0.500	-0.446	0.655
Standard	1.265	0.271, 2.510	0.556	2.276	0.023
High	1.861	0.946, 3.068	0.527	3.531	< 0.001
Fallow	0.811	-0.311, 2.117	0.601	1.349	0.177
(c) Cicadellidae	AIC = 141.26				
(Intercept) extra-tussock	1.792	1.411, 2.130	0.183	9.814	< 0.001
Standard	-0.944	-1.609, -0.330	0.324	-2.918	0.004
High	-0.602	-1.155, -0.062	0.277	-2.173	0.030
Fallow	-0.223	-0.769, 0.312	0.274	-0.815	0.415
(d) Delphacidae	AIC = 99.52				
(Intercept) extra-tussock	-0.916	-2.711, 0.211	0.707	-1.296	0.195
Standard	2.526	1.329, 4.347	0.730	3.459	< 0.001
High	2.862	1.693, 4.673	0.721	3.968	< 0.001
Fallow	1.099	-0.369, 3.019	0.816	1.346	0.178

There was no relationship between sward height and the abundance of Cicadellidae however there was a strong relationship observed with Delphacidae (Figure 5.3.7). When the numbers of Delphacidae was corrected for sward height to give a relative density, the effect of fertiliser can be explored independently of sward height effects. No significant effect was found between the high and standard fertiliser applications; the difference in effect between the two treatments was negligible (Table 5.3.5 and Figure 5.3.7)

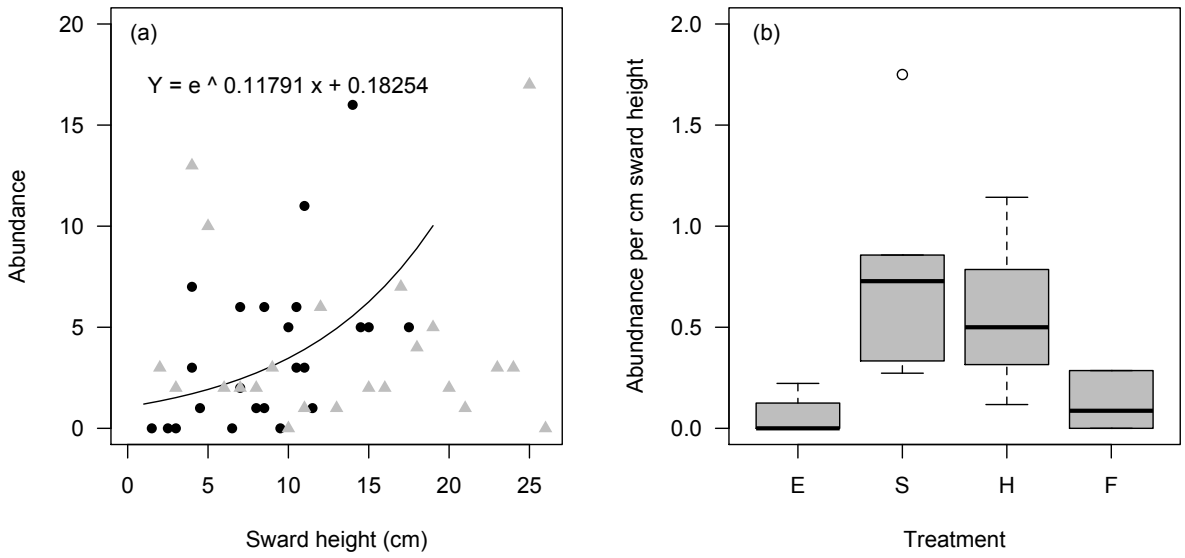

Figure 5.3.7: Relationship between sward height and numbers of Delphacidae and Cicadellidae. (a) circles show delphacids and triangles cicadellids. Delphacids show a significant positive relationship between sward height and abundance ($F_{1,22} = 6.57, P = 0.02, R^2 = 0.24$ solid black line) cicadellids do not. The line of best fit was provided from a GLM with a Poisson error structure and a log link. R^2 calculated taking $1 -$ (residual deviance / null deviance)(b) the density of Delphacidae ($n/swardheight$) by treatment. Letters stand for E – extra tussock, the area outside a tussock, S – a single fertiliser application, H – a high, double fertiliser application and F – fallow tussocks.

Table 5.3.5: Generalised linear model of the density of Delphacidae ($n/swardheight$) for each of the treatments, a Gaussian model was used, with an identity link.

	Estimate	95% CI	SE	t	p
Extra tussock(Intercept)	0.069	-0.241, 0.380	0.159	0.438	0.666
Low fertiliser	0.709	0.288, 1.130	0.215	3.301	0.004
High fertiliser	0.497	0.090, 0.904	0.208	2.392	0.027
Fallow	0.062	-0.377, 0.502	0.224	0.277	0.784

Using NMDS community differences were significantly predicted by treatment effects ($F_{3,20} = 3.278, R^2 = 0.33, p = 0.009$), which ran with a final stress of 0.15. Observations of *R. imitans*, *J. dubia* and *Species 1* (The unidentified cicadellid nymph) however, appeared to show no correlation between treatment type, attributed to low numbers observed. *Anoscopus serratulae*, and *Zyginidia scutellaris* were associated strongly with all fertiliser treated tussock treatments. *Neophilaenus lineatus* and *Arthaldeus pascuellus* to fallow and extra (out of tussock) treatments. *Streptanus spp.* was also associated with the extra tussock treatments (Figure 5.3.8).

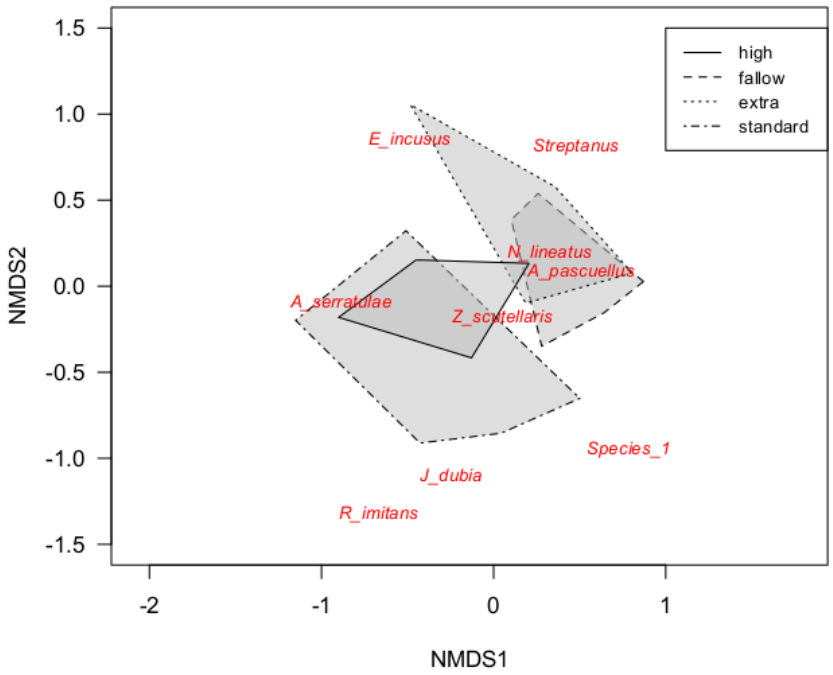

Figure 5.3.8: Non metric multidimensional scaling plot demonstrating, the community differentiation within each of the different treatments. The different treatments are; *high* those with a high level of fertiliser treatment, *fallow* those with no fertiliser, *extra* the extra-tussock samples, outside of tussocks and *standard* those with a standard level of fertiliser application. Red text shows genus and species abbreviations for Auchenorrhyncha, nymphs and adults were included. Species 1 is a first instar unidentified Deltocephalinae nymph. Polygons illustrate dissimilarities in species composition by treatment, non-overlapping polygons are the most dissimilar.

5.4 Discussion

The previous chapter outlined how the plant community studied was dominated by just one plant species, i.e. *S. arundinaceus*. However, within this largely homogeneous community, there is a heterogeneous habitat structure. This heterogeneity is maintained, in part, by the presence of tussocks. In other systems tussocks provide a buffer for grassland biodiversity; tussocks of *Holcus lanatus* and *Dactylus glomerata* - both common on this study site - are known to play host to a wider biodiversity of beetles than in their non tussock states (Luff, 1966; Tscharntke & Greiler, 1995). However on this site, only *S. arundinaceus* formed tussocks, which are known to be of lower quality grazing material (Nihsen *et al.*, 2004). Tussocks are less preferable to a range of grazing animals, having high endophyte levels (Putnam *et al.*, 1991; Bacon & Siegel, 1988; Rudgers & Clay, 2007) and considered invasive by some sources, dominating and out competing other grasses (Spyreas *et al.*, 2001). However, it is possible that the role of tall fescue is a dominant driving force in maintaining sward structural heterogeneity is important to insect communities, in spite of the grass species being less desirable from a habitat management and grazing perspective.

In this chapter interaction terms in models similarly demonstrated the potential benefits of tussocks; as sward heights are reduced the positive influence of tussocks increases in line with the hypotheses. When compared to the broader grassland habitat, they provide better shelter, and microhabitat conditions than surrounding swards (Waterhouse, 1955; Purvis & Curry, 1981). Moreover, protection from predation may be better provided in these comparatively dense structures (Barnes *et al.*, 1995). This pattern was similar to those reported by Helden *et al.* (2010) that highlighted the importance of cattle dung islets (tussock like structures) in shorter grazed swards. At

Coe Fen however, there is no external nutrient input to natural tussocks; in fact unimproved tussocks may be less nutritionally rich when compared to the surrounding sward matrix (Pengelly *et al.*, 2006). Tussocks in cut meadows may also be beneficial as a buffer against management through cutting, as they are denser than the surrounding swards (Dennis *et al.*, 2001), and density is less affected by cutting whilst being more important than sward length. Seasonal cutting reduces the blade length of grass. However, cutting had very little effect on the sward height of tussocks. Moreover, sward height as opposed to blade length had the strongest positive response from insects, which is probably directly linked to vertical height and increasing sward density, as opposed to the length of single blades, which can sit at varying angles in a sward matrix.

Improvement in host plant quality has measurable effects on feeding preference and performance (Awmack & Leather, 2002; Hartley *et al.*, 2003; Littlewood, Stewart & Woodcock, 2012). However, the effect of nutrient input and structure are not independent of each other (Dittrich & Helden, 2012). Nutrient input is proportional to plant growth (Miles, 1958; Ingestad, 1977; Dittrich & Helden, 2012) and by proxy the amount of *living space* in improved swards is increased for the majority of insects that they play host to (Prestidge, 1982*a*; Morris, 2000). Moreover, increased nutrient input would lead to more growth and so more energy fixed and available to cascade up food chains (Bukovinszky *et al.*, 2008). However, as the experiment was conducted over a short period of time, it is less likely that such trophic relationships would have extended beyond the primary producers and their consumers, thus highlighting further that it is more to do with free choice in Auchenorrhyncha over shorter time scales (e.g. Prestidge 1982a).

Fertiliser input increases nitrogen in plant tissue as well as promoting growth (Sedlacek *et al.*, 1988). In these experiments fertiliser may have increased species richness initially, however further nutrient availability, may not have increased the number of consumer species; potentially even reducing it within some treatments. This is supported by some long term studies on grassland Auchenorrhyncha where improvement increases numbers of individuals but not always species richness over time; *simplifying* the insect community, in favour of a few dominant species (Haddad *et al.*, 2000). The contrasting responses of cicadellids and delphacids could be explained by nutritional demands. Different groups move to specific nitrogen levels in grass, cicadellids preferring less nutrient rich swards than delphacids (Prestidge, 1982*a*,*b*; Prestidge & McNeill, 1983).

Models in this study suggested that although delphacids were correlated with increasing sward height and density, cicadellids responded to sward length (length of individual blades), and were found to be more abundant outside of tussocks. This could be related to the feeding positions of the different families, delphacids being generally more epigeal than cicadellids (Waloff & Solomon, 1973). It is possible that dense swards with shorter blade length could provide suitable habitats for delphacids, with cicadellids feeding further up plants, thus requiring extra length in blades. Conversely, both groups have a diverse suite of predators and parasites (Singh *et al.*, 1993) which the structure of tussocks could exclude (Barnes *et al.*, 1995). Cicadellids however, may be better equipped than delphacids outside of this microhabitat when avoiding predation; in part because of their tendency towards macropterous forms, and not sacrificing flight for productivity as readily as delphacids (Denno *et al.*, 1989; Nickel, 2003). However, predator avoidance behaviour in Auchenorrhyncha is not limited to flight: the Cer-

copoidea (froghoppers or spittle bugs) have the best jumping performance of any insect described (Burrows, 2003), closely followed by cicadellids and then delphacids, potentially because of morphological constraints (Burrows & Sutton, 2008). Thus the delphacids in this study may benefit more from denser and longer swards provided by tussocks than their cicadellid counterparts, at least from a predator-prey interaction perspective.

Schedonorus arundinaceus is a common plant that has an ecological tendency towards tussock formation (Brock *et al.*, 1997), it is also the sole host plant of *R. imitans*. Host plant specificity is a familiar and potentially beneficial characteristic trait in rare Auchenorrhyncha species (den Bieman, 1987; Nickel & Remane, 2002), as it increases the probability of encountering potential mates where conspecifics are at low density (Bayram & Luff, 1993; Cherrett, 1964; Dennis *et al.*, 1998, 2001; Luff, 1966). It is quite common for rare monophagous planthoppers, for example *Metropis latifrons* (Kbm.), *Eurysanoides douglasi* (Scott.), *Chloriona sicula* Mats., *Kelisia halpina* Remane to be monophagous on tussock forming plants (Nickel & Remane, 2002; Holzinger *et al.*, 2003; Stewart & Bantock, 2015). *Doratura impudica* Horvath, is monophagous on *Elytrigia juncea* (Fisch.), preferring sparse pioneer vegetation on sand dunes (Stewart & Bantock, 2015). Although, not tussock forming the low density of plants in this habitat would increase probability of conspecifcic heterosexual encounters of this rare species. Therefore, it is possible that it is a combination of host specificity and habitat specificity that enables persistence of these rare species. Conversely, common delphacids in Europe are generally more oligophagous, in the first or second degree; feeding on one or multiple families of plant (Nickel & Remane, 2002).

5.4.1 Summary

Tussocks are important for Auchenorrhyncha communities and rare species, they maintain heterogeneity in grassland, as they increase available microhabitat niches, especially where there is limited plant diversity. Moreover, they potentially increase the probability of heterosexual conspecific encounters of rare species, providing an important link between host plant ecology and low density populations. These small populations are at greater risk, and the relationship between host plant and tussock microhabitat could explain the persistence of some species at lower population densities than others. Although not rare on this study site, *R. imitans* is still rare throughout its range, thus an optimal habitat with an abundance of its tussock forming host plant could explain its persistence, at least at this local level. Conversely those patterns observed with leafhoppers and planthoppers may translate to other species, thus tussocks could be responsible for the persistence of many species in grasslands.

Chapter 6

Direct and indirect interactions between *Ribautodelphax imitans* and other species

6.1 Introduction

Previous chapters highlighted potential interactions between *Ribautodelphax imitans* and other species, notably *Javesella pellucida*. This was illustrated by overlapping life cycles, co-abundance patterns year to year, shared host plants and fidelity towards similar grassland structures. If interactions between species occur it is important to understand whether they are mutualistic or antagonistic, or indeed if they are neutral.

Studies of competition between closely related insects are common but responses are varied. Research focussed on its effect on fecundity (McClure, 1980), growth and development (Price *et al.*, 1980; Müller *et al.*, 2001), habitat selection (Whitham, 1978), microhabitat choice (niche shifting) (Ferrenberg & Denno, 2003; Sun *et al.*, 2009) and survival (Akimoto, 1988; Mcclure,

1990). Competitive interactions are often asymetric in the insect herbivore community in which there is one competitor with a strong advantage over the other (Denno & Kaplan, 2007; Denno *et al.*, 1995). Therefore competitive interactions may not be obvious in field data. However, interactions between herbivores are not always antagonistic. Facilitative interactions have been measured in some species, with survival, body size and growth rate positively affected (Forrest, 1971; Kidd *et al.*, 1985; Damman, 1989; Ohgushi, 2008). In some cases this is due to increased nutrient availability caused by previous feeding of another species (Forrest, 1971; Kidd *et al.*, 1985), although such facilitative relationships with sap-sucking insects are comparatively rarer than those involving chewing guilds (Denno *et al.*, 1995; Denno & Kaplan, 2007). Chewers promote re-growth, a more nutritious food source, thus enabling this facilitative relationship (Damman, 1989). However, such interactions are can be transient and can lead to stronger competitive interactions later as the density of one species increases to a detriment of the other (Flamm *et al.*, 1987; Denno *et al.*, 1995).

There were differences in laboratory development between *R. imitans* and *J. pellucida* (Chapter 3). However, the reasons for these differences were not obviously apparent from the outset. The developmental rate of insects can be affected by conspecifics, sometimes negatively and sometimes positively (Forrest, 1971; Kidd *et al.*, 1985; Damman, 1989; Denno *et al.*, 1995; Ohgushi, 2008). In gregarious species, some benefit is afforded to synchronous development (such as facilitative feeding), where an optimal level is met, above total isolation but below an overcrowding limit (Bentley, 1944; Ishii, 1963; Wharton *et al.*, 1967; Youdeowei, 1967). As insects were housed individually in the ex-situ development experiments, and isolation may have affected their developmental rates, therefore differences between

the development of *J. pellucida* and *R. imitans* in the lab may be an artefact of this. Experiments were designed to test this, and it was hypothesised that there would be both an effect of conspecifics and heterospecifics on development times.

Although *R. imitans* was restricted to just the one host plant, the developmental rates of generalists can vary tremendously between hosts, because of the varying ability of insects to get nutrition from different plants (Hough & Pimentel, 1978; Bethke *et al.*, 1991). However, the ability of the specialists in deriving nutrition from their hosts may be potentially better than generalists. Therefore, when both generalist and specialist interact there is potential for competition. The direction of this competition however is more commonly deleterious to monophagous species, because they are less able to move from one host plant to another (Karban, 1989; Denno *et al.*, 1995), although some authors would debate this, and state that specialists are competitively superior on their hosts, leading to a disadvantage to the generalist (Long *et al.*, 2007). The importance of this for grassland communities could therefore be quite far reaching, especially when there is a limited number of host plants partitioned within a community of generalists and specialists. This chapter also seeks to clarify, whether one species can affect the host plant utilisation of another when sharing resources, using the two model species *R. imitans* and *J. pellucida* - the commonest co-occurring delphacid with *R. imitans* on Coe Fen. It was hypothesised that *R. imitans* because of its host plant specialism, may have a competitive advantage over a generalist species therefore it may influence both host plant utilisation. Moreover the presence of other species on its host was thought to have a limited effect on developmental rates because of this advantage.

6.1.1 Aims

1. Determine the extent to which the development of *R. imitans* is affected by conspecifics or allospecifics.

2. Undertake experiments to understand whether a specialist has a competitive advantage over resources that may be shared with other species, and whether their presence can modify host plant utilisation patterns. The generalist *J. pellucida* and the specialist *R. imitans* are used as models.

6.2 Methods

All experiments followed the same same protocal where plants were grown from seed 500 ml clear plastic cups containing 5cm John Innes no.3 potting compost. A section of 5 μm nylon mesh netting was affixed to the top of the cups to prevent insect escape (Figure 6.2.1). All grass species were grown from seed (approximatley 10 seeds) and thinned to just three plants two weeks before experiments, and all had three tillers before the insects were added. Insects were checked at least once every day. All experiments were conducted in controlled temperature conditions at 17°C; 16 hours light, eight hours dark (L16:D8) under full spectrum artificial lighting.

Figure 6.2.1: Photograph of the clear plastic containers used in the experiments. With mesh affixed to the top, and plants enclosed. Diameter at the top of the container was 12 cm and the base 12 cm, height was 14 cm.

6.2.1 Conspecific effects on *R. imitans* development

In these experiments third instar nymphs were used, because of timings between generations of insects and laboratory usage at the time. Insects were removed from culture plants using a paintbrush and then placed in their experimental containers to be reared on *S. arundinaceus*, at densities of one, five and 10 individuals per container. The total time to adulthood was used as a measure of development time. There were six replicates for each density. The densities of insects and number of replicates were chosen because of the amount of available insect material at the time.

6.2.2 Intra and inter-specific effects on *R. imitans* development

In order to determine whether the developmental times of either *R. imitans* or *J. pellucida* were affected by each other an experiment was set up in which there were either six *R. imitans* ($n = 5$), six *J. pellucida* ($n = 6$) or six of each species in the same container (12 individuals) ($n = 6$). There were a total of 17 replicates. Insects for these experiments were added at the third instar stage. As densities of insects in allospecific treatments were higher than single species treatments this enabled the testing of a second hypothesis, that a lack of difference in development time between the species in mixed treatments could indicate no competition between the two species. Moreover, the difference in density between mixed and single species treatments could be justified because of the lack of density effect found in the previous experiment (Section 6.2.1). The densities of insects and number of replicates were chosen because of the amount of available insect material at the time.

Performance of *J. pellucida* on different host plants

Using eight replicate containers each of *S. arundinaceus*, *Holcus lanatus*, *Agrostis stolonifera* and *Dactylus glomerata*, single second instar *J. pellucida* were added to each container after being carefully removed from culture using a paintbrush, just one individual per container was used in this case to avoid any possible conspecific effects. The instar of each individual was recorded daily for the duration of the experiments.

6.2.3 Competition-mediated host plant choice

This experiment was designed to determine whether there was an effect of feeding by the specialist *R. imitans* on the host plant choices made by the the generalist *J. pellucida*. To do this, two plant species were used *S. arundinaceus* and *H. lanatus*. The latter plant was chosen because it was the second most common plant on Coe Fen, and one which *J. pellucida* had a strong positive response to. *Schedonorus arundinaceus* was chosen because of the host plant relationships with *R. imitans*.

Using containers identical to the previous experiments *S. arundinaceus* and *H. lanatus* seeds (approximately 10) were planted 3cm apart in the same containers. Plants were thinned to one plant each, and the experiments started when plants had three tillers of growth. At this point, groups of either 10 *R. imitans* or *J. pellucida* were added to a container. There were 8 containers of *J. pellucida* and 8 containing *R. imitans* and both plant species in each container. The host plant choices were recorded after 48 hours in *J. pellucida*. After one week the *J. pellucida* were removed from their plants with a paint brush and added to the containers with *R. imitans*. The proportion of individuals on either plant was recorded in both cases.

In an alternative treatment eight groups of 10 *J. pellucida* were allowed to establish themselves on plants and the host plant choices recorded after 48 hours, one week following this period of establishment 10 *R. imitans* were added to these same containers, and the host plant choices of *J. pellucida* were again recorded 48 hours following this introduction. For each treatment there were eight replicates per treatment *J. pellucida*.

6.2.4 Statistical methods

In group rearing experiments developmental time of *R. imitans* or *J. pellucida* were modelled using generalised linear mixed effects regression modelling (GLMER). Models included the random effects 'cage' which accounted for any variation within rearing containers:

$$\bar{y} \approx \text{test conditions} + (1|cage)$$

Models used a Poisson error structure and a log link between the parameter estimate and the mean of the distribution. Poisson error structures were used because of the count data and unequal variance. The *R* package lme4 was used in GLMER analysis (Bates *et al.*, 2015).

Experiments which looked at proportion of individuals on plants, used parametric t-tests with 95% confidence limits estimated around the mean. One way analysis of variance was used, to test for host plant performance in *J. pellucida*. All data was tested for normality using a Shapiro Wilk test.

6.3 Results

6.3.1 Conspecific effects on development of *R. imitans*

Models illustrated no effect of density on *R. imitans* development ($F_{2,18} = 0.56, P > 0.58$; Table 6.3.1). Back-transformed estimates from the model (Table 6.3.1) suggested development times of 18.5 days (95% CI = 8.9, 38.2) for one individual, 16.2 days (95% CI = 8.8, 29.69) at densities of five individuals and 14.9 days (95% CI = 8.8, 29.8) at densities of 10, but no density dependent effect. There was however a much greater range in development times between individuals at high densities (of 5 and 10 individuals), this range extending into shorter elapsed times to adulthood (Figure 6.3.1).

Table 6.3.1: The outputs of a linear mixed effects model comparing the development times of *R. imitans* at different densities. Models had 18 degrees of freedom, and used a Poisson error structure and a log link between the parameter and the mean of the distribution. Intercept is labelled (int.).

Density	Parameter est.	95% CI	S.E	t	p
1 (int.)	2.918	2.639, 3.198	0.142	20.481	< 0.001
5	-0.133	-0.469, 0.202	0.171	-0.779	0.436
10	-0.219	-0.635, 0.197	0.212	-1.032	0.302

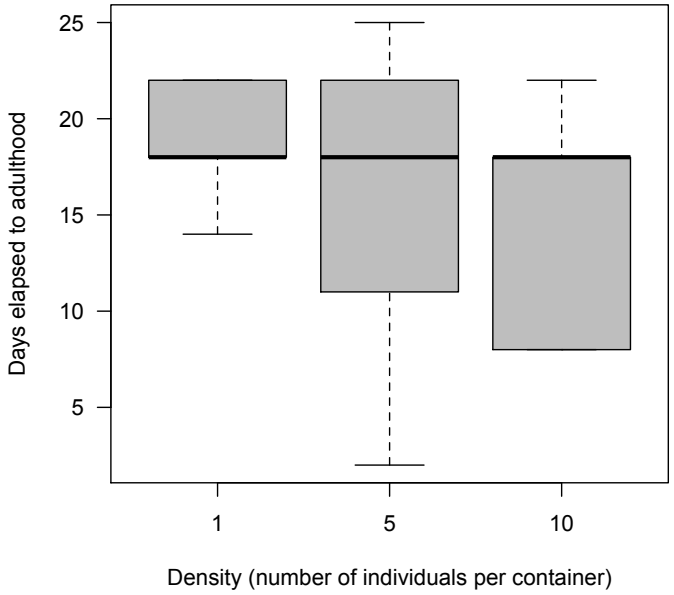

Figure 6.3.1: The number of days elapsed from third instar to adulthood in *R. imitans* in rearing contains with densities of 1, 5 and 10 individuals.

6.3.2 Interspecific effects

Models illustrated there was no effect of allospecifics on developmental time of *R. imitans* ($F_{2,11} = 0.264, p > 0.77$; Table 6.3.2 a) or *J. pellucida* ($F_{2,11} = 0.051. p = 0.95$; Table 6.3.2 b) (Figure 6.3.2). There was again a much greater range of development times observed with *R. imitans* compared to *J. pellucida* (Figure 6.3.2)

Table 6.3.2: The outputs of a linear mixed effects model measuring the effect of allospecific presence on the number of days to adulthood of (a) *R. imitans* and (b) *J. pellucida*. Totals of six individuals were used per cage in controls and 12 in tests. Treatments were therefore in ratios of 1:1 conspecifics to allospecifics or 1:0 conspecifics to allospecifics. Models have 12 degrees of freedom and use a Poisson error structure with a log link between parameter estimates and the mean of the distribution. The absence of the second species was modelled as the intercept.

	Parameter est.	95% CI	SE	z	p
(a) *R. imitans*					
J. pellucida absent	3.346	3.197, 3.495	0.076	43.954	< 0.001
J. pellucida present	-0.146	-0.382, 0.091	0.121	-1.208	0.227
(b) *J. pellucida*					
R. imitans absent	3.294	3.207, 3.381	0.044	74.532	< 0.001
R. imitans present	0.014	-0.110, 0.138	0.063	0.225	0.822

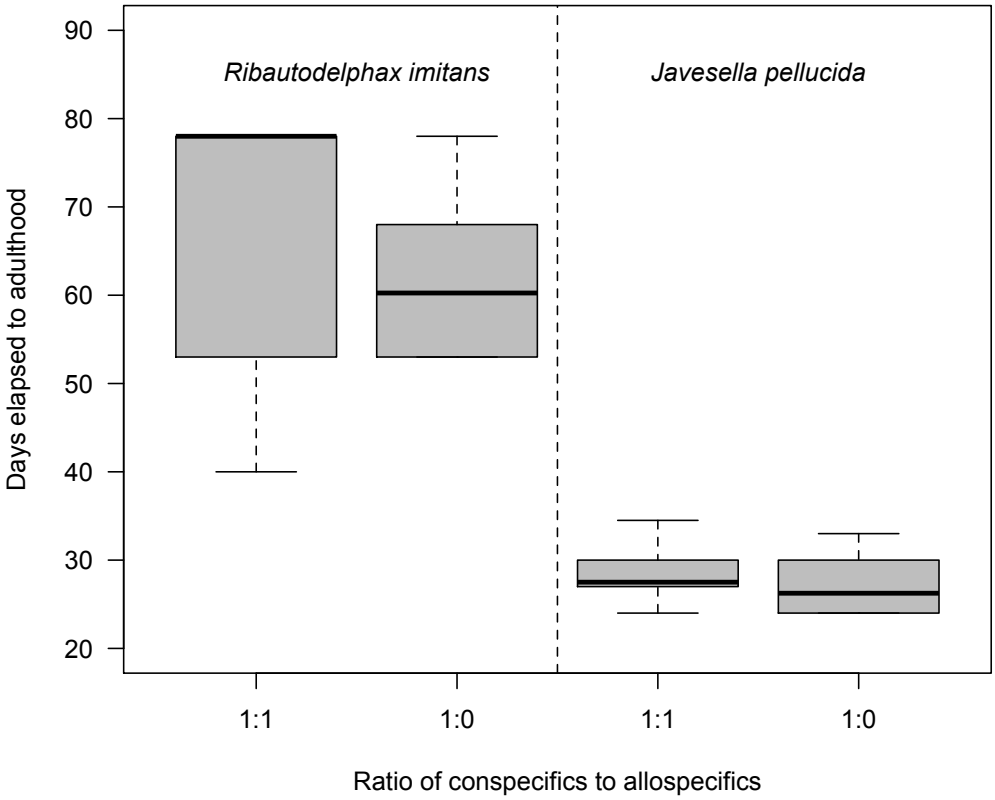

Figure 6.3.2: The number of days elapsed from second instar to adulthood in *R. imitans* and *J pellucida* in both mixed species and single species groups of 6 individuals total, ratios of 1:1 conspecifics to allospecifics and 1:0 conspecifics to allospecifics.

6.3.3 Performance of *J. pellucida* on different host plants

There was no significant effect of host plant on the developmental rate of *Javesella pellucida* ($F_{3,15} = 0.96, P = 0.43$) (Figure 6.3.3). There was slight variability between plants, although no obvious effect was apparent that could be attributed to any of the host plants. The range of develop-

mental times on *S. arundinaceus* was narrower than on other plant species (Figure 6.3.3).

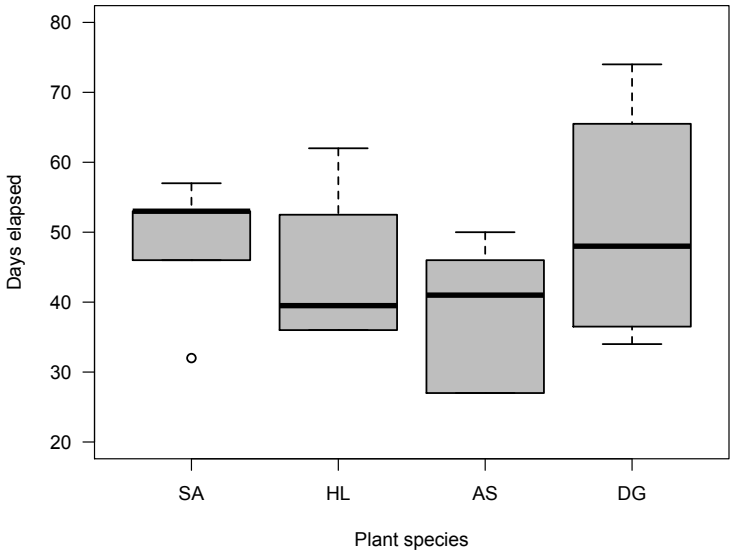

Figure 6.3.3: The total amount of time taken to reach adulthood *J. pellucida* on different host plants. The codes for the plant types correspond to SA - *Schedonorus arundinaceus*, HL - *Holcus lanatus*, AS - *Agrostis stolonifera* and DG - *Dactylus glomerata*.

6.3.4 Competition-mediated host plant choices

Experiments were designed to test whether the choices of one species - the generalist - could be mediated by the specialist.

Javesella pellucida showed an overall choice preference for *S. arundinaceus* where a mean proportion of 0.66 (95% CI = 0.57, 0.75) individuals were counted, compared to *H. lanatus* where mean proportions of 0.34 (95%

CI = 0.25, 0.43) individuals were counted. A significant difference of 0.32 (95% CI = 0.26, 0.57; $t_{26} = 5.45, P < 0.001$; Figure 6.3.4 a).

Overall preference for *S. arundinaceus* changed with *J. pellucida*, in experiments where *R. imitans* where already established on plants. When *J. pellucida* were housed in single species groups, proportions 0.35 (95% CI = 0.26, 0.44) were found on *H. lanatus*. When they were added to the experimental arenas where *R. imitans* where already established there was a marked preference for *H. lanatus* and proportions of 0.77 (95% CI = 0.63, 0.91) individuals were found on this plant species compared to the alternative. A significant difference in proportions of 0.41 (95% CI = 0.35, 0.77; $t_9 = 13.70, p < 0.001$; Figure 6.3.4 b).

There was however no difference in the proportions of *J. pellucida* on alternate host plants before and after the addition of *R. imitans* to experimental arenas where *J. pellucida* were already established a non-significant mean difference of 0.06 (95% CI = -0.12, 0.54; $t_{14} = 0.60, p = 0.559$; Figure 6.3.4 b).

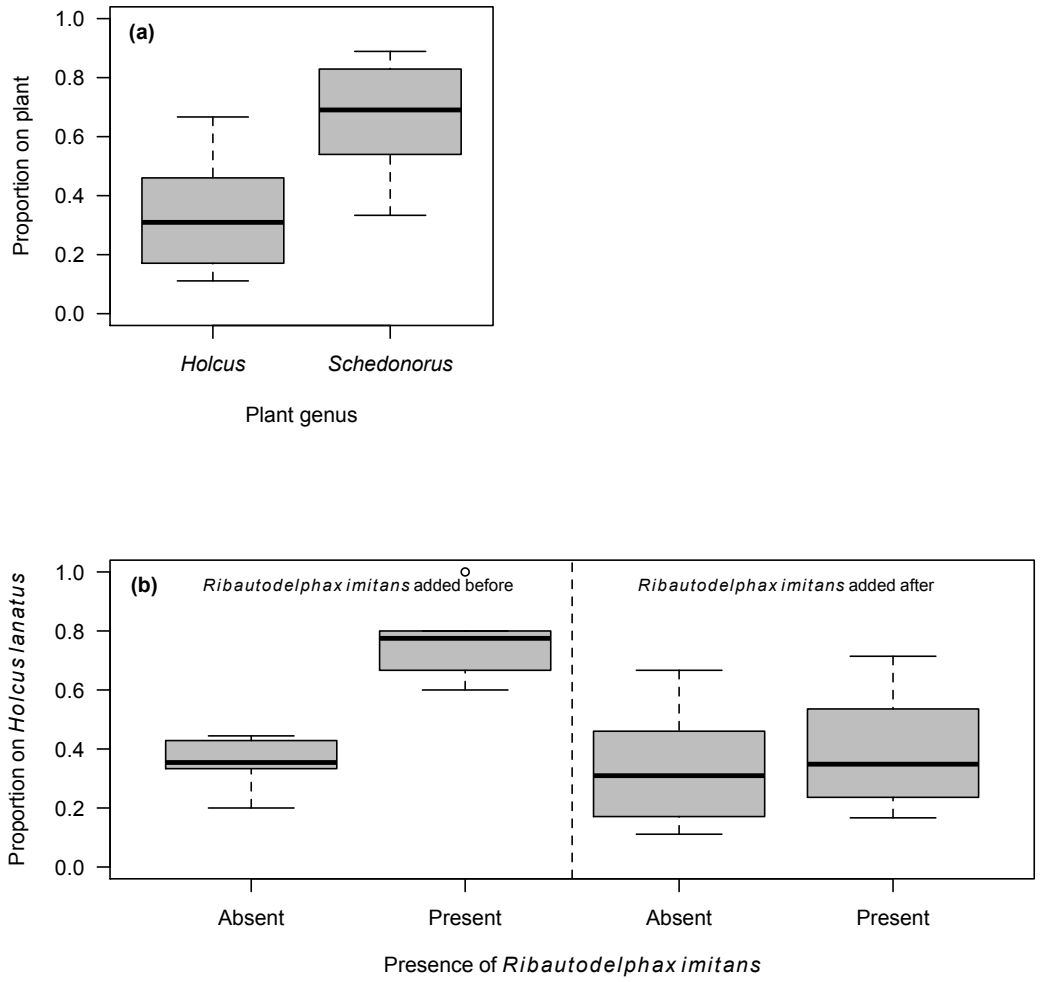

Figure 6.3.4: Effect of presence of *R. imitans* on host plant choice in *J. pellucida*. Two plant choices were given *Holcus lanatus* and *Schedonorus arundinaceus*. (a) the verall preference of *J. pellucida* for either *S. arundinaceus* or *H. lanatus* expressed as a proportion of individuals for either plant ($n = 16$). (b) The proportions of *J. pellucida* on *H. lanatus* in experiments where *R. imitans* were established prior to addition of *J. pellucida* ($n = 8$) or where *J. pellucida* were established first prior to the additon of *R. imitans* ($n = 8$). Boxes compare treatments where *R. imitans* were either present or absent.

6.4 Discussion

6.4.1 Conspecific and allospecific effects on development in *R. imitans*

There appeared to be no significant effect of allospecifics on developmental rate, however a skew in the data tended towards higher developmental rates with increased *R. imitans* density. Although the conspecific density effect was not significant the data may suggest a pattern that, given greater statistical power, could be detected. Moreover, there was no effect of allospecifics on the development of either *R. imitans* or *J. pellucida* in line with the hypothesis.

Synchronous development is very important in terms of host plant herbivory as it ensures that populations peak when the best resources are available for feeding and reproduction, such as oviposition (Watt, 1987; Ivashov *et al.*, 2002). In mass emergent insects such as Ephemeroptera, some beetles and cicadas, synchronisity can flood predators (safety in numbers) and ensures heterosexual encounters of adults (Corkum *et al.*, 1997; Marshall, 2001; Kojima, 2015). Positive conspecific density-dependent effects on development are potentially beneficial for species with low population sizes, as matched developmental rates ensures sexually mature adults are phenologically synchronised.

The density of individuals in cages with allospecifics was greater than experiments without. The lack of any measured effect in this case could illustrate that either there was no competition between the two species on the same plant, or the two species had differentiated niches. Niche differentiation by phloem feeding may be less distinct as comparisons between other guilds such as chewing versus sucking, as all phloem is connected through the plant's vascular system (Inbar *et al.*, 1995). Phloem feeders can however, partition

resources between each other, although this differentiation may be far less obvious; mechanisms such as different feeding sites and differences in stylet length allow this coexistence (Hajek & Dahlsten, 1986; Inbar & Wool, 1995; Dixon, 2012); the lack of effect seen in these experiments potentially due to similar niche partitioning.

6.4.2 Evidence of competition mediated host switching in generalist herbivores

Host plant switching competition experiments clarified that although plant networks may contain a variety of different sources shared out between generalists and specialists, the specialists can possibly modify the host plant choice that generalists make which supports the hypothesis. Previous experiments did not suggest any negative effect of development induced by other species when no plant choice was given; this is possibly because a resource limiting threshold was not reached for either species. In phytophagous sap sucking communities resources are rarely limiting, however this does not necessarily mean that competition is not occurring (Denno & Kaplan, 2007). The species may compete for resources, at a level not easily measured by developmental changes but are enough to drive host plant choice.

In host plant performance experiments using *J. pellucida*, there appeared to be no differences in development time on any of the plant species. However, there did appear to be a preference for *S. arundinaceus* in choice experiments when offered the alternative plant *H. lanatus*. One explanation could relate to plant defences, as the stems of *H. lanatus* are relatively hairy compared to *S. arundinaceus* (Streeter *et al.*, 2009). Hairs on plants evolved as an anti-predatory defence, and it is possible that they put off the nymphs feeding when an alternative, more glabrous, host plant is available (Levin, 1973;

Karban & Agrawal, 2002). Other textural components such as differences in diameter and stem thickness could also be attributed to this.

Host plant utilisation preferences in generalists were affected by specialists in these experiments when the specialist was established on plants prior to introduction of the generalist, but not the other way round. Data suggest that the egg incubation periods for *J. pellucida* were longer than that of *R. imitans* with both species in the field overlapping as adult generations (Chapter 3 - section 1.6.1). This supports the idea that nymphs of *R. imitans* establish on host plants prior to the onset of the dominant generalist *J. pellucida* if females of both species are ovipositing at the same time.

There are examples of closely related species in different systems competing because of temporal overlap (Towns, 1983; Karban, 1986; Inbar *et al.*, 1995; Ferrenberg & Denno, 2003). Competition is often mitigated by species by being temporally asynchronous, such as with Delphacidae and Cicadellidae (Waloff & Solomon, 1973; Waloff, 1980). However, competition can still occur if one species directly follows the other in time. Previous feeding of one planthopper species can negatively affect the performance of the next species feeding on the same plant (Denno *et al.*, 2000). However, there have been no other studies that have investigated feeding of a specialist on the plant choice of a generalist in this way. It is possible that this particular generalist-specialist relationship is a strong force in structuring insect communities, as it would drive local patterns of resource utilisation. The early establishment of *R. imitans* could guarantee it a competitive advantage on its host plant. Shorter egg incubation duration in this case could be the mechanism underpinning this advantage.

6.4.3 Summary

Addicott (1978) stated that in order for interspecific competition to occur certain criteria needed to be fulfilled. Firstly, intra-specific competition needed to be obvious in the species studied, secondly, the species needed to be spatio-temporally synchronous and, lastly, the fitness of one species is decreased by the presence of the other. In these experiments it was determined that there was no effect of either species on the other's fitness, nor was there any obvious intra-specific competition, in spite the two species being spatio-temporally synchronous. However, in spite of this there was compelling evidence to suggest that the host plant choices of one species can be influenced by the other. It is possible that this may lead to either a competitive advantage of one species, or a reduction in direct competition that could affect the fitness of the other species.

Chapter 7

General Discussion

7.1 How does the ecology of *R. imitans* relate to its rarity?

This thesis investigated *Ribautodelphax imitans*, an insect rare in the UK. It highlighted that although rare in terms of range, a species can be relatively common at a local scale, raising the questions, when is a species rare and is *R. imitans* actually rare?

Rarity can be principally explained by three factors: habitat specialisation, when a species has very specialised habitat requirements that are seldom catered for; habitat restriction, where its range is restricted; or simply one species' population can be a smaller size than others in its community (Rabinowitz *et al.*, 1986; Gaston, 1994; Cunningham & Lindenmayer, 2005). *Ribautodelphax imitans* was never the dominant species in its community on Coe Fen, although moderately high numbers were recorded.

Proportionally *R. imitans* had consistently lower population sizes on Coe Fen than the commonest delphacid *J. pellucida*, therefore in particularly

bad years it is possible that this species goes through periods of very low population density (See chapter 3, monitoring of Coe Fen). For example in 2012 where no summer *R. imitans* were found, in spite of finding limited numbers of *J. pellucida*. Local population extinction, could be a particularly serious problem for low density populations, as when one local population goes extinct recolonisation is a lot less likely from other sites, however exact population estimates are hardly ever without bias and precise population estimates are hard (MacKenzie *et al.*, 2003).

Ribautodelphax imitans was found in abundance in an MG12 mesotrophic grassland (a habitat type not mentioned previously in relation to *R. imitans*(Kirby *et al.*, 1992*b*; JNCC, 2010)) , and it was dependent upon tall fescue (Chapter 4) with high fidelity towards the tussocks this grass forms (Chapter 5), indicative of habitat specialism. UK records are still limited as are those in mainland Europe, suggesting it is rare in other areas of its range, although there is some indication that in Germany that the species is becoming more widespread (personal communication with Herbert Nickel, April 2016).

Terrestrial communities are often dominated by a few common species, with the bulk of species rare (Gaston, 2008; Mouillot *et al.*, 2013). One reason for this is that communities may be affected by a continuous flow of migrants, and the balance between those transient and core species will determine the species abundance distribution (Southwood, 1996; Magurran & Henderson, 2003). When some species' population size reaches a critically low level, it falls into an extinction vortex, whereas others may persist at these much lower relative population sizes (Gabriel & Bürger, 1992). One of the principal problems with living at low density, in sexually reproductive species, is finding conspecifics for reproduction. Therefore, the size of such

populations is obviously critical in determining the establishment of any insect species on a new site (Day *et al.*, 2004), ultimately affecting population status. The Allee effect (Allee & Bowen, 1932) explains how, as populations reach low density, their growth rate decreases around a critical point at which population growth is limited, be this by unavailability of mates, or death rate exceeding birth rate (Stephens *et al.*, 1999). Given the possibility of an Allee effect, is it feasible that *R. imitans* is influenced by such processes? Potentially ecological characteristics could enable species' to flourish at otherwise low population densities, but what are those characteristics?

One positive characteristic that enables the persistence of smaller populations is host plant specificity. Monophagy can come about for a number of reasons, normally these are directly related to plant chemistry and defence (Cates, 1980, 1981), however factors independent of palatability can lead to monophagy, for example structures such as hairs that reduce palatability (Woodman & Fernandes, 1991). Insects select plants as they provide optimal microhabitat, for example grass tussock structures (Dennis *et al.*, 1998, 2001); moreover these often denser structures then in turn provide refuge from predation (Smiley, 1978; Bernays, 1988), then as these herbivores select for palatability, they lose the ability to feed on other hosts from their evolutionary past (Smiley, 1978). In the case of *R. imitans* the species is monophagous on tall fescue, which is a tussock–forming plant that provides a suitable refuge from predation and sub–optimal climate conditions (Barnes *et al.*, 1995). The consequence of these ecological specialisations to microhabitat and host plant, have far reaching consequences for small population sizes. Feeding on a single host restricts the local range of conspecifics, aggregating them to higher local densities, thus increasing the probability of co-occurrence with other sexes. Some plant species have very specific

growth forms, such as tussocks which are less favourable for vertebrate grazers (Putnam *et al.*, 1991; Bacon & Siegel, 1988; Rudgers & Clay, 2007), and provide suitable microhabitat refuges in otherwise short swards as they maintain a stable environment in spite of heavy management and grazing pressure (Chapter 4; Luff *et al.*, 1966; Dennis *et al.*, 1998, 2001; Dennis 2003; Helden *et al.*, 2010). When the ecology of Auchenorrhyncha is examined in greater detail, particularly with delphacids, similar traits observed in *R. imitans* are apparent in other rare species for example *Metropis latifrons* and *Eurysanoides douglasi*(Nickel & Remane, 2002; Holzinger *et al.*, 2003), suggesting that the persistence of rare species can be secured by adopting similar life history strategies, such as being monophagous on tussock forming grasses (Nickel & Remane, 2002). Of course, this is a double-edged sword in some cases, because being restricted to just one host means that if that host disappears so does the specialist herbivore (Stork & Lyal, 1993; Dunn *et al.*, 2009).

Ribautodelphax imitans' competitive ability, may also be a factor in its persistence at a local level. Its life histories are synchronous with other species on the same host plant, and on those hosts it is able to influence the host plant choices made by a generalist species (*J. pellucida*) that shares these resources (Chapter 6). However, whether this ability would translate into relationships with other specialists is unknown. There are limited species that feed solely on tall fescue (Nickel, 2003) and it is unknown as to whether any of these exist within the natural range of *R. imitans*.

Smaller population densities are less likely to exert large stresses on the plants they feed, avoiding a reduction in plant health or increase in anti–herbivore defence. Additionally, specialised parasite populations are unlikely to be supported by a low density of hosts (Doutt & Nakata, 1973; Anderson &

May, 1978). Some species may be rare in terms of occourance, but not necessarily in terms of numerical abundance. A classic example in the hemipteran community can be observed with periodical cicadas *Magicicada* spp. which are abundant above ground in years when emergent but the majority of their life is spent as subterranean nymphs, not at risk from the same suite of terrestrial predators, as other terrestrial hemipterans (Marshall, 2001). The temporal synchronicity of periodical cicadas upon emergence ensures mating success, and inundation of predators. However, their relative rarity in time prevents adaptive synchronicity from these terrestrial predators, and parasites; these benefits would also be afforded species that is relatively infrequently encountered.

In spite of the gene-centered view of evolution (selection acting on the individual rather than at the group level) now being widely uncontested (Dawkins, 2006), the idea of a wider 'extended evolutionary synthesis', where selection acts on the group level, is adopted by some in the scientific community (Laland *et al.*, 2014). The concept of adaptation to rarity as an ecological strategy may be controversial, on the basis that it could be thought of as group-centric. However I propose it as merely rarity being less disadvantageous to some species than others on account of their life histories.

7.2 Why protect rare insects?

The term ecosystem-services (ES) is an important term in the UK, with significant revenue spent on the protection of species that give something to human society. In particular biocontrol agents and pollinators are valued as being of paramount importance to crop security. By 1998 the value of pollination services by bees to the UK economy was thought to be around

130 million for outdoor and 30 million pounds for indoor crops (Carreck & Williams, 1998) This figure rose to around 620 million pounds in 2015 (Knapton, 2015). These natural resources or services provided by nature, give economists and conservationists alike something to work with.

Auchenorrhyncha found in grasslands typically feed on the grass species found there, rather than the associated shrubs and dicotyledonous plants (Nickel & Remane, 2002). This study highlighted the potential of tall fescue dominated grasslands with low floristic diversity for the conservation of one such priority species. It is possible this species has specific niche and habitat requirements, that may not be met should those meadows be managed for more economically valuable ecosystem service providers (such as bees). During a transition from a low quality tussock sward to a mixed sward with many dicot species managed for pollinators, many of the resources for the predominantly grass feeding Auchenorrhyncha would be lost. With a growing concern for habitats, food security and an increasing population is there any room for protecting species should they not provide any tangible benefit, in terms of the services they provide?

Auchenorrhyncha are a group with potentially limited potential in terms of value to stakeholders as an ecosystem service provider (Costanza *et al.*, 1997). Leafhoppers and planthoppers are not classically valuable as they do not provide roles such as pollination, which can be economically costed. Their value as a food source for beneficial predators such as insectivorous birds (Whelan *et al.*, 2008) and as hosts to bio-control agents (Doutt & Nakata, 1973), or their overall contribution to biodiversity (Figure 7.2.1), should not however, be understated. Auchenorrhyncha are a useful indicator group for groups such as ecologists and developers, given our present taxonomic knowledge, and how they quickly respond to to disturbance, age and

overall quality of habitats (Andrzejewska, 1962; Nickel & Hildebrandt, 2003; Hollier *et al.*, 2005; Moir & Brennan, 2007). Moreover, all biodiversity has a value, albeit not always tangible, and these cultural values (e.g. aesthetics) should not be discounted, for their lack of obvious commercial appeal (Chan *et al.*, 2012) (Figure 7.2.1). Although making the case for cultural values is tough for insects, owing to a lack of general interest (Leather, 2009).

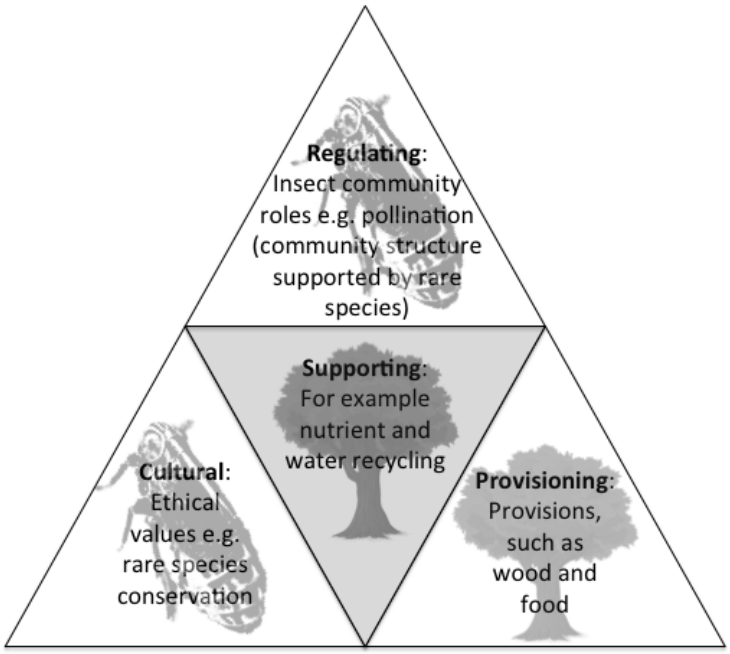

Figure 7.2.1: Ecosystem goods and services, segmented pyramid diagram. Illustrating the four defined areas for ecosystem services; regulating, supporting, provisioning and cultural.

A 2013 report by the Association of Chartered Certified Accountants (ACCA), Fauna and Flora International and accountancy firm KPMG identified that financially accounting for natural capital is of paramount importance (Bon-

ner *et al.*, 2012). However, one principal issue arising from this concept is that in conventional economics, where there are no substitutes, increasing scarcity of a resource also increases its value (Victor, 1991), such is the case with some natural resources, such as some rare insects that attract collectors (Slone *et al.*, 1997). Although with no commercial appeal and limited interest in Auchenorrhyncha, maybe the opposite case is true, and rare species with cultural, less tangible value strengthens the argument for conservation, as increasing rarity increases awareness of important habitats (Prendergast *et al.*, 1993).

Leather (2009) wrote at length on the disparity of funding between vertebrate and non-vertebrate research. In spite of the taxonomic dominance of insect groups over the world, scientific funding is often geared towards more popular groups with more of a public profile (such as charismatic megafauna, birds and other mammals). In spite of insects having this monetary value that can be attributed to them in terms of ecosystem services, research and public profile they are still undervalued. However, multidisciplinary projects are making the case for undervalued insects. The New Forest Cicada Project (http://newforestcicada.info) is one such example, in which smart phone technology is used to passively monitor for *Cicadetta montana* (Zilli *et al.*, 2014). This project is stirring interest not only in the ecological world but also the technological community. Perhaps these multidisciplinary approaches to science can generate more interest in insects. These so called *change agents* (Snaddon *et al.*, 2013) engage collaboration with different members of the scientific community. Technologies such as ispot (www.ispotnature.org), and other internet based nature recording technologies, for example the Ladybird Recording Scheme app (www.ladybird-survey.org), have helped turn a nation of passive nature admirers into nature recorders. When this effort

on recording is coupled with advertising revenue from these technologies and wider public engagement there is potential for value, outside of their obvious links to ecosystem services. Therefore balancing the two monetary and aesthetic values. In the UK there are limited technological resources for Auchenorrhyncha recording although there is a comprehensive pictoral guide available (www.britishbugs.org.uk) and the recording scheme has its own website (www.ledra.co.uk). However, whether that will lead to more of an engagement with this particular group of understudied insects remains to be seen.

Arguably if we value nature purely on tangible ES then what value are rare insects? Rare insects make a much smaller contribution to the overall population size of a group and are therefore less important in terms of their service provision. However, that aside, the importance of rare species for overall ecosystem function and the health of the community as a whole should not be understated. Lyons and Shwartz (2001) provided an interesting experimental synthesis of the importance of rare species. There are far more rare species in a community compared to dominant ones, but removing an equivalent amount of rare species in plant communities increased susceptibility to disruption from invasive species (Lyons & Schwartz, 2001).

7.2.1 Why should we be concerned about *R. imitans* and other Auchenorrhyncha in the UK?

Schröter *et al.* (2014) argued that the ecosystem services concept emphasises multiple benefits of ecosystems to humans, facilitating collaborations between scientists and other stakeholders. The utilitarian nature of the ES approach is not accepted by all, with some stating, that it condones an exploitative relationship with nature swaying public opinion away from a biocentiric view

(appreciating nature on its intrinsic values) to an anthropocentric one (in which nature is appreciated solely on its instrumental value) (McCauley, 2006; Sagoff, 2008; Redford & Adams, 2009). This obviously raises problems for rare species conservation. However, a compromise could be made in that rare species are important for biodiversity, and that biodiversity in itself is an ecosystem service; its different components (e.g rare species) underpin ecosystem conditions and processes influencing ecosystem service provision (Balvanera *et al.*, 2006; Cardinale *et al.*, 2006; Hector & Bagchi, 2007). The frameworks used by the Millennium Ecosystem Assessment have acknowledged overlaps between biodiversity and ecosystem services by including aspects of biodiversity within the habitat, supporting, and cultural service categories (De Groot *et al.*, 2012; Schröter *et al.*, 2014). Therefore, anything that contributes and maintains biodiversity within some ecosystems is in itself an ecosystem service by definition. Therefore the conservation of any rare species, irrespective of its functional role (as an ecosystem service) is important and the loss of any species can have negative effects on the health of an ecosystem. Therefore, whether or not *R. imitans* is threatened, it is a specialist, and not understanding its requirements in its habitat could have negative impacts on its population and so the wider community.

7.3 Does *R. imitans* deserve its status?

Ribautodelphax imitans represents one of a small number of conservation priority Auchenorrhyncha in the UK. From what is known following this work, is this status deserved? Historic records of the species date back to those from Dorset in 1959. Are more recent records evidence of the species spreading, or is it indicative of a poor recording effort?

The rate of spread of naturally colonising insects is not as readily reported as more economically interesting data on invasive and novel pest insects (Kirk & Terry, 2003; Brown *et al.*, 2008). Increased recording effort could determine whether the species is widespread but not usually locally common, or restricted in its habitat range. However, without intensive and focused effort from national recorders, it unlikely that detailed questions on distribution will be answered soon. That said, the case for *R. imitans* has raised issues of the importance of Auchenorrhyhncha conservation and whether a focused effort on their conservation can be justified, when there is a limited input from general recording of their distributions in the UK.

There are a few Auchenorrhyncha species in the UK that are rapidly spreading, *Asiraca clavicornis* being one such species. This species was historically recorded as having a wide distribution throughout southern England, but by 1992 it was only known in the Thames Estuary region, however the species appears to be undergoing a recent expansion (Kirby *et al.*, 1992*b*; Jones & Hodge, 2010), indicating it has gone through a period of population contraction and expansion. Detailed understanding of its ecology and habitat requirements may have improved records. Kirby (1992) described this species as ruderal grassland specialist associated with tussocks, however recent data indicates bindweeds (Convolvulaceae) as hosts (BRC, 2016). This is a simple error to make, because bindweeds are sometimes found growing around taller grass tussocks, often unnoticed (Dittrich & Helden, 2012). Other more generalist species however, such as *Athysanus argentarius*, are known to have undergone recent expansions in the UK (Salmon *et al.*, 2000). *Zyginella pulchra* is another species, recorded once in 2002 but by 2007 was found to have an almost national distribution (Bleicher *et al.*, 2007; Stewart *et al.*, 2009). This illustrates insects undergoing expansions can go rather unnoticed in the

UK until they are relatively well established. There are possible explanations for this however, *Z. pulchra*, is found on sycamore in its growing season (Wilson & Mühlethaler, 2013) moving to evergreens such as Leyland cypress *Cupressus* spp. as it overwinters (Stewart *et al.*, 2009). If we observe that it is switching from a native plant as a nymph, to a less frequently sampled non-native as an adult, it is possible that the species was under-recorded, as the host plants were simply ignored by recorders and the nymphs were comparatively hard to identify (Wilson & Mühlethaler, 2013). Current publications on its ecology in the UK however may have alerted recorders to its presence and host plant ecology, thus leading to a recent influx of records. Furthermore, this highlights the importance of ecological knowledge when studying any species distribution, rare or otherwise, extremely pertinent to the topic of this thesis.

The 2011 Auchenorrhyncha survey of Coe Fen represents one of the most comprehensive studies of Auchenorrhyncha, and community datasets sent to the UK recording scheme. For the majority of the UK only sporadic records have been received, therefore the likelihood of encountering any species that has low frequency within its community is small. Out of the 1765 10km^2 records submitted to the scheme, only 376 of these areas received more than 50 records. The majority of 10km^2 squares have less than 100 records (1549) most of these less than 50 (1380) (Figure 3.5.2). The bulk of high recording density was situated in Dorset, Hampshire, Greater London and Kent regions.

With what is known about the population size of *R. imitans* at Coe Fen, and the number of submissions to the UK Auchenorrhyncha recording scheme, the probability of any new records coming to light are small. When it is considered that just 520 records of *J. pellucida*, one of the commonest

if not the commonest delphacid in the UK, have been submitted to the UK Auchenorrhyncha recording scheme new records of rare species are unlikely.

Additionally, sites where *R. imitans* was found may be unfavourable to recorders or habitat types that are harder to sample. The bulk of insect records come from casual recorders, or recorders without specialised recording equipment. In this study a suction sampler was used, which is a far more efficient way of extracting insects than other more conventional methods, such as sweeping (Brook *et al.*, 2008), particularly in tussocky swards which *R. imitans* appears to favour. Perhaps with a more focused specialised effort nationally, a more accurate population distribution for *R. imitans* will be clarified.

7.3.1 Revisiting the biodiversity action plan for *R. imitans*

The original biodiversity action plan (BAP) (JNCC, 2010) for *R. imitans* highlighted a lack of knowledge of its community, its habitat and host plant associations in the UK. This thesis has clarified that MG12 mesotrophic grasslands can support stable populations of this species, a different habitat type to that highlighted in the original BAP (JNCC, 2010). Moreover, it is monophagous on tall fescue. Community associations show a co–abundance with other delphacids, particularly *J. pellucida*. Further investigation of the direct interactions between *R. imitans* and others in its community could highlight the nature of its rarity or the frequency with which it is recorded. The co-abundance patterns with *J. pellucida* illustrate that targeted sampling during adult generations of more dominant delphacids such as *J. pellucida*. particularly around tall fescue tussocks, may return more records of this species. Potentially *R. imitans* is a species tolerant of small population

sizes relative to others in the community, and only with focused sampling efforts at the right time, and in the right microhabitat would more records come to light.

The BAP (JNCC, 2010) and JNCC UK conservation review published by JNCC (Kirby, 1992) both emphasised chalk grassland as the habitat for *R. imitans* and that this species had very specific habitat requirements, not readily catered for in the UK. Over improvement of grassland, and a dominance of scrub in favour of mixed grassland sward from decline of rabbit populations due to myxomatosis were both cited as potential risks, as was over management from cutting. One could hypothesise that limited cutting, or the cutting practised on Coe Fen, posed a limited threat to *R. imitans*, or potentially even enabled it to flourish. Long-term studies could elucidate the real long term effects of different management regimes. However, with a species known on so few sites, experimental work is not always feasible. The importance of tall fescue grass within a matrix of other species, particularly when that matrix forms a series of tall tussocks, cannot be understated however, as tussocks can reduce the effect of cutting by providing refuge for invertebrates (Luff, 1966; Bayram & Luff, 1993; Dennis *et al.*, 1998, 2001).

7.4 Summary and conclusions

This project has investigated a broad range of related aspects of the ecology of *R. imitans* and its associated community; the position of *R. imitans*, associated host plant interactions and micro-habitat effects on Auchenorrhyncha as well as potential interspecific competition. The study highlighted the importance of a matrix of tussocks in a floristically poor habitat, and how these structures can help maintain of generalist and specialist Auchenorrhyncha.

The study also highlighted how direct host plant linkages can reinforce insect communities from species loss and how they maintain biodiversity, although they are perhaps less important than habitat structure for Auchenorrhyncha. It also brought to light how these structures and related host plant associations may be important for the persistence of low–density populations. It was demonstrated how *R. imitans* and possibly other specialists could mediate the host plant choices of generalists, potentially mitigating direct competition at an advantage to the specialist. However there is still room for a great deal more work on both *R. imitans* and around the conceptual framework of this thesis. There are still gaps in our understanding of rare species and their community ecology; of what enables rare species to persist and what makes them rare. Further developmental studies of *R. imitans*, in particular whether there are any allospecific and conspecific effects on development, could help elucidate some of the issues explaining such rarity. Further experiments exploring density dependence and microhabitat use could be designed with a view to developing a more comprehensive understanding as to how and why some rare species persist and some do not. The methods developed in this study could be useful in future studies in these areas. Furthermore, this project highlighted information gaps in the recording of Auchenorrhyncha in the UK, and a necessity for more comprehensive efforts in the future. Researchers often do not find it desirable or practical to look for rare insects, with some exceptions (such as butterflies (New, 1997), and simply ignoring them due to a lack of desire, logistics or commercial appeal would be a loss to science.

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Appendix 1

Table A.1: Auchenorrhyncha species that were collected on Coe Fen during twice yearly sampling, during April and July. The first letter of the month is given preceded by the date.

Species	A-11	J-11	J-12	A-13	J-13	A-14	J-14	A-15
J. pellucida	156	156	11	2	296	80	761	131
E. incisus	25	134	9	21	33	5	32	5
Z. scutellaris	7	2	98	10	48	8	11	5
R. imitans	12	11		3	21	9	19	2
J. dubia	4	17	3			6		
A. serratulae		20			7			
S. sordidus		15	10			1		
A. pascuelis		9					14	
A. makarovi		17			3		1	
P. spumaris		1	2		6		2	
E. aurata		9	1					
M. viridigriseus							7	
P. cephalotes		6						
N. lineatus		1			1		3	
D. pulicaris		3						
E. urticae		1	1		1			
E. aurata							2	
A. albifrons			2					
C. quadrinotata		1						
D. stylata		1						
E. notata		1						
M. attenua		1						
M. sexnotatus		1						
R. adumbrata		1						
R. coronifer		1						
S. lugubrina		1						

Appendix 2

Entomologica Austriaca

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The community ecology of *Ribautodelphax imitans* (Ribaut, 1953) (Hemiptera: Delphacidae), a rare UK planthopper in a distinct grassland habitat

A.D.K. Dittrich & A.J. Helden

Abstract: *Ribautodelphax imitans* (Ribaut, 1953) (Hemiptera: Delphacidae) is a rare planthopper throughout its recorded range, and in the UK where it is afforded conservation priority status. Following the discovery of this species on a site in Cambridgeshire, UK in 2010 a study was designed to understand the population status of *R. imitans* and its place in the Auchenorrhyncha community structure. The species was found not to be rare within the community – in fact it was one of the most abundant delphacids on the site. However, the community was dominated by *Javesella pellucida* (Fabricius, 1794). Although the reason for the general rarity of *R. imitans* on a national scale is still unclear, evidence from the community structure suggests that strong interspecies interactions between other species that it is phenologically synchronous with may be a factor.

Key words: Auchenorrhyncha, insect conservation, rarity, interspecific interactions, phenology

Citation: Dittrich A.D.K. & Helden A.J. 2016: The community ecology of *Ribautodelphax imitans* (Ribaut, 1953) (Hemiptera: Delphacidae), a rare UK planthopper in a distinct grassland habitat. – Entomologica Austriaca 23: 87–95.

Introduction

Auchenorrhyncha (Insecta: Hemiptera) are an abundant grassland insect group, although little consideration is afforded them with research often focused on more charismatic insects such as butterflies and moths (Lepidoptera) (Pawar 2003). In spite of this, leafhoppers and planthoppers have key roles in ecosystem function. For example, they form a valuable part of passerine birds diet (Buchanan et al. 2006). More recently, they have been recognised as important indicator species, particularly in grassland and forest systems (Hollier et al. 2005, Moir & Brennan 2007), as they respond quickly to changes in environmental factors (Sedlacek et al. 1988, Dittrich & Helden 2012, Helden et al. 2010).

In the UK, the Auchenorrhyncha fauna is mainly composed of leafhoppers (Cicadellidae) (296 species) and planthoppers (Delphacidae) (75 species). Although there are representatives from the Cixidae (12 species), Aphrophoridae (9 species), Membracidae (2 species), Issidae (2 species), Cercopidae (1 species), Cicadidae (1 species), and Tettigometridae (1 species) (Stewart & Bantock 2015). The numbers of species on the UK list however

Fig. 1: A female of *Ribautodelphax imitans*.

is quite dynamic, with many new additions in recent years. Since 2007 seven species have had been added to the UK fauna. These include *Delphax crassicornis* (Panzer, 1796), *Psammotettix helvolus* (Kirschbaum, 1868), *Oncopsis appendiculata* Wagner, 1944, *Zygina nivea* (Mulsant & Rey, 1855), *Macropsis megerlei* (Fieber, 1868), *Dryodurgades antoniae* (Melichar, 1907) and *Pithyotettix abietinus* (Fallén, 1806) (Skidmore 2008, Maczey & Masters 2009, Ramsay 2010, Bantock et al. 2010, Bantock 2011, Bantock 2012, Denton 2012).

Historically Auchenorrhyncha have not been recognised the same level of protection as higher vertebrates (Myers et al. 2000, Biedermann et al. 2005) and other more charismatic insects such as the greater stag beetle *Lucanus cervus* (Coleoptera), and many butterflies (Lepidoptera). However there are a small number of Auchenorrhyncha considered conservation priorities, based on the now defunct Biodiversity Action Plan (BAP), which has now been replaced within a Joint Nature Conservation Committee JNCC framework. These species are: *Cicadetta montana* (Scopoli, 1772) the UKs only true cicada (Hemiptera: Cicadidae), restricted to the New Forest and now believed to be extinct, *Erotettix cyane* (Boheman, 1845) the pondweed leafhopper, restricted to just three sites in the UK, *Doratura impudica* Horvath, 1897, *Euscelis venosus* (Kirschbaum, 1868), *Eurysanoides douglasi* (Scott, 1870), *Chlorita viridula* (Fallén, 1806) and *Ribautodelphax imitans* (Ribaut, 1953) (Fig. 1), the target species in this study.

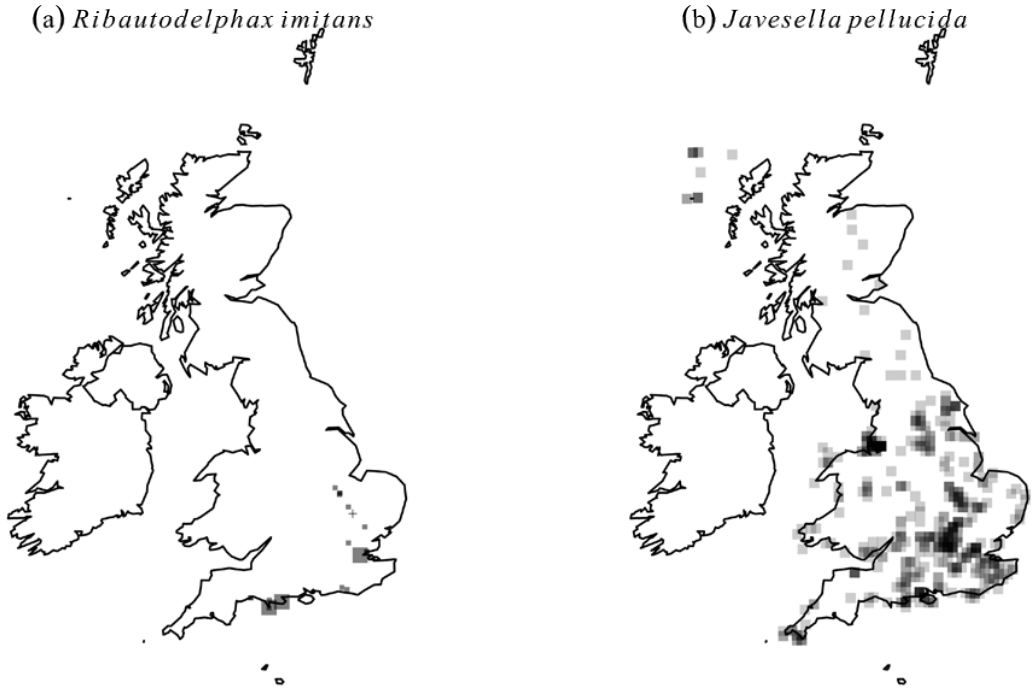

Fig. 2: The UK distribution of (a) *Ribautodelphax imitans* and (b) *Javesella pellucida*.

Historically *R. imitans* was only recorded from Dorset and Devon (1959 and 1969). The species was then rediscovered in Dorset in 1997 and then again in 2000, there was also a single report from East Sussex in 1998. Following these discoveries there were some scattered observations of the species in Middlesex (2000), Essex (2006–2013), Northampton (2013), Lincolnshire (2013), Peterborough (2013) and most recently three sites in Cambridgeshire which include Coe Fen, Needingworth Quarry and Devils Dyke (2011–2015) (Fig. 2a). However, records do need to be taken with some caution, as insect records are often patchy and suffer from under-recording (Dunn 2005) without the resolution of higher taxa such as mammals (Ceballos & Ehrlich 2006). This aside, predictions of insect distributions can be made (Hassall 2012). Arguably the most common planthopper in the UK is *Javesella pellucida* (Fabricius, 1794) and even though its dominance in surveys illustrates this commonness, there is still a large proportion of the UK not covered by *J. pellucida* records (Fig. 2b). In many areas this is likely to be due to lack of recording and reporting, – rather than it actually being absent. Therefore estimates on *R. imitans* distributions need to be considered with caution. However, notwithstanding under-recording, the species is considered rare in other parts of its range (Nickel & Remane 2002).

In 2010 *R. imitans* was found on Coe Fen Cambridgeshire (N 521158.39°, E 0000658.77°), a meadow covering approximately 6.6 hectares of cattle grazed land on the banks of River Cam, close to the historic city centre of Cambridge. A field study was designed for 2011 to understand more about its community ecology, and ecological position. Here we describe a field study in 2011 and present detail regarding its ecological position within the Auchenorrhyncha community.

Material and methods

The site was notionally divided up into 10 plots from which four subsamples were taken (totalling 40) samples every two weeks from April – October 2011. Each sample was collected with a Vortis suction sampler (Arnold 1994) and consisted of 10 sixteen-second sucks (Brook et al. 2008), covering a total area of 0.2 m² (10 × 0.02 m²). Each sample was emptied into a sweep net and then a pooter used to collect all adult Hemiptera for preservation in AGA (alcohol-glycerine-acetic acid) solution (Gibb & Oseto 2006) and later identified to species using identification keys of Le Quesne (1960, 1965, 1969), Le Quesne & Payne (1981), Biedermann & Niedringhaus (2009) and Kunz et al. (2011).

Results

The sampling caught 7178 Auchenorrhyncha (leafhoppers, planthoppers and allies) from 43 species. Out of this sample, the majority were either Cicadellidae (leafhoppers) or Delphacidae (planthoppers) – although far fewer of the latter were collected. Of all these species, six have local status, and two were nationally scarce; notable A (occurring in 30 or fewer 10km squares) and notable B (occurring in 31 – 100, 10km squares). *Ribautodelphax imitans* – the focus of this study – and the rarest species is designated a Red Data Book (RDBK), Biodiversity Action Plan (BAP) 2007 and Natural Environment and Rural Communities (NERC) S.41: priority action species.

Coe Fen was dominated by less than 15 species; the majority recorded less than 25 times through the course of the field season. *Ribautodelphax imitans* however, was one of the more abundant species ranking seventh out of all Auchenorrhyncha recorded. The Shannon's equitability index was 0.603 suggesting a normal, moderately diverse community. In addition Whittaker plots were also used to determine evenness of species rank distributions within the community; they illustrated percentage abundances were typically low for most species (less than 1 %). Although plots suggest normal species distributions; shown by the moderate decline in log abundance with increasing rank. Slopes for all combined species, Delphacidae and Cicadellidae were -0.16 respectively (Fig. 3). Of all the delphacids on Coe Fen, *J. pellucida* was the most abundant; this species equating to ~36 % and 50 % of all delphacids sampled on Coe Fen, compared to *R. imitans* which had an overall abundance of ~3 %. *Arthaldeus pascuellus* (Fallén, 1826) was the commonest auchenorrhynchan overall, with 2431 specimens around 33 % of the total number of individuals or 50 % of all cicadellids.

Sampling illustrated differences in life cycles between the two main groups of Auchenorrhyncha: planthoppers showed a June-July peak whereas cicadellids had a July-August peak population with smaller peaks approximately eight weeks previous in each group. The life cycle of *R. imitans* (Fig. 4a) appears to mirror that of other delphacids. In 2011 there were two peaks; a late peak in June-July, preceded by an earlier – much smaller – April peak. At the late peak 91 individuals were found (14th July 2011) and at the earlier just 12 individuals were sampled (21st April 2011), a three sample average abundance of 48 and 9 respectively. The life cycles of other Auchenorrhyncha were also modelled, and the justifications for those species based on the total abundance of each species, in this case the nine most abundant species life cycles were observed. The profiles of each species

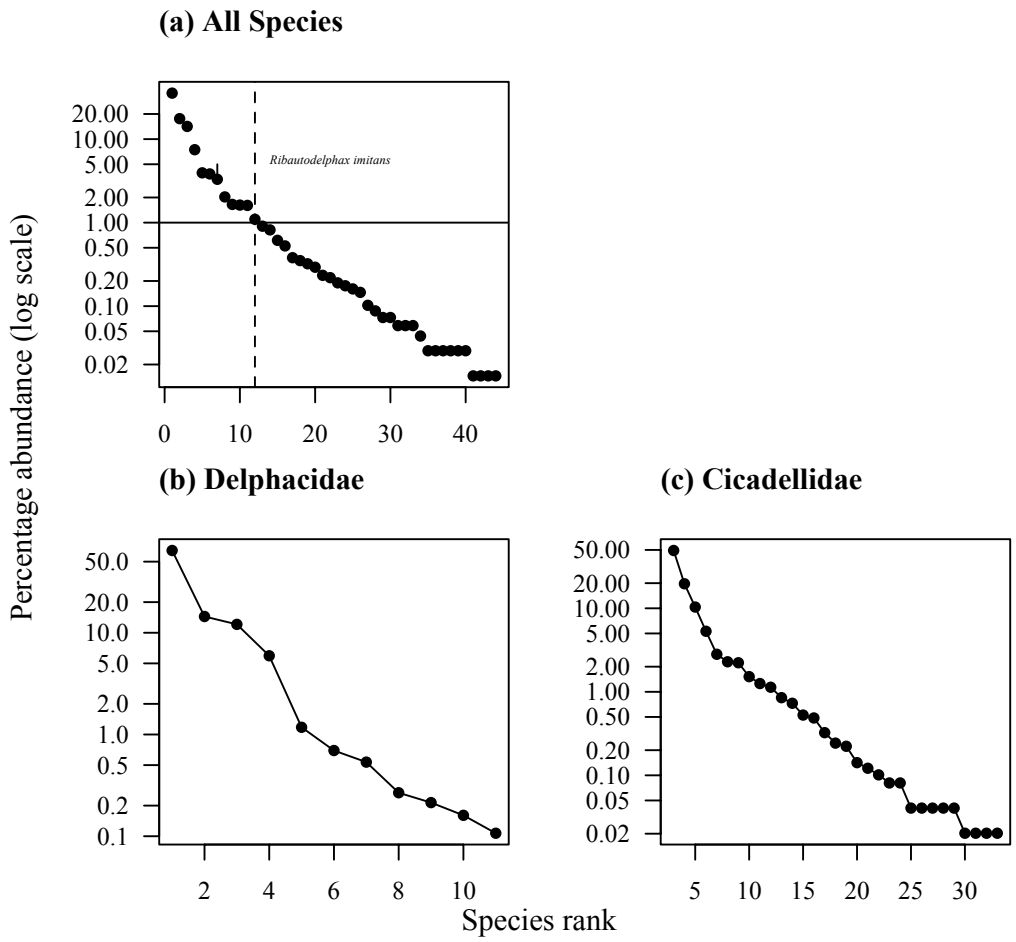

Fig. 3: Percentage rank abundance of (a) all Auchenorrhyncha on Coe Fen. (b) Delphacidae and (c) Cicadellidae grouped separately. *Ribautodelphax imitans* is represented on (a) with a small arrow.

are shown in figure 4: (b) *Javesella pellucida*, (c) *Arthaldeus pascuellis*, (d) *Zyginidia scutellaris*, (e) *Javesella dubia*, (f) *Euscelis incisus*, (g) *Muellerianella fairmairei*, (h) *Anoscopus serratulae*, (i) *Streptanus sordidus* and (j) *Deltocephalus pulicaris*. The majority of species were bivoltine, with the exception of *Z. scutellaris* which had three generations, and *A. serratulae* which appeared to have just one.

Discussion

Rarity is not caused by one universal factor – there are many reasons for it. Within a community, species can be numerically rare (lower abundance than allospecifics), rarity can be mediated by habitat specificity, and geographically species can be widespread or restricted (Cunningham & Lindenmayer 2005). Within communities species may not be numerically abundant; the majority of species are rare when compared to the dominant few – but are they in fact rare? In this study *R. imitans* is a potential example of one species that is locally abundant (albeit not dominant) but restricted in its range for some reason. The exact reasons for the rarity of *R. imitans* are unknown.

Although rarity is commonplace, the reasoning behind persistence of rare species through space and time is not always so simple. Potentially rare species can only persist if their

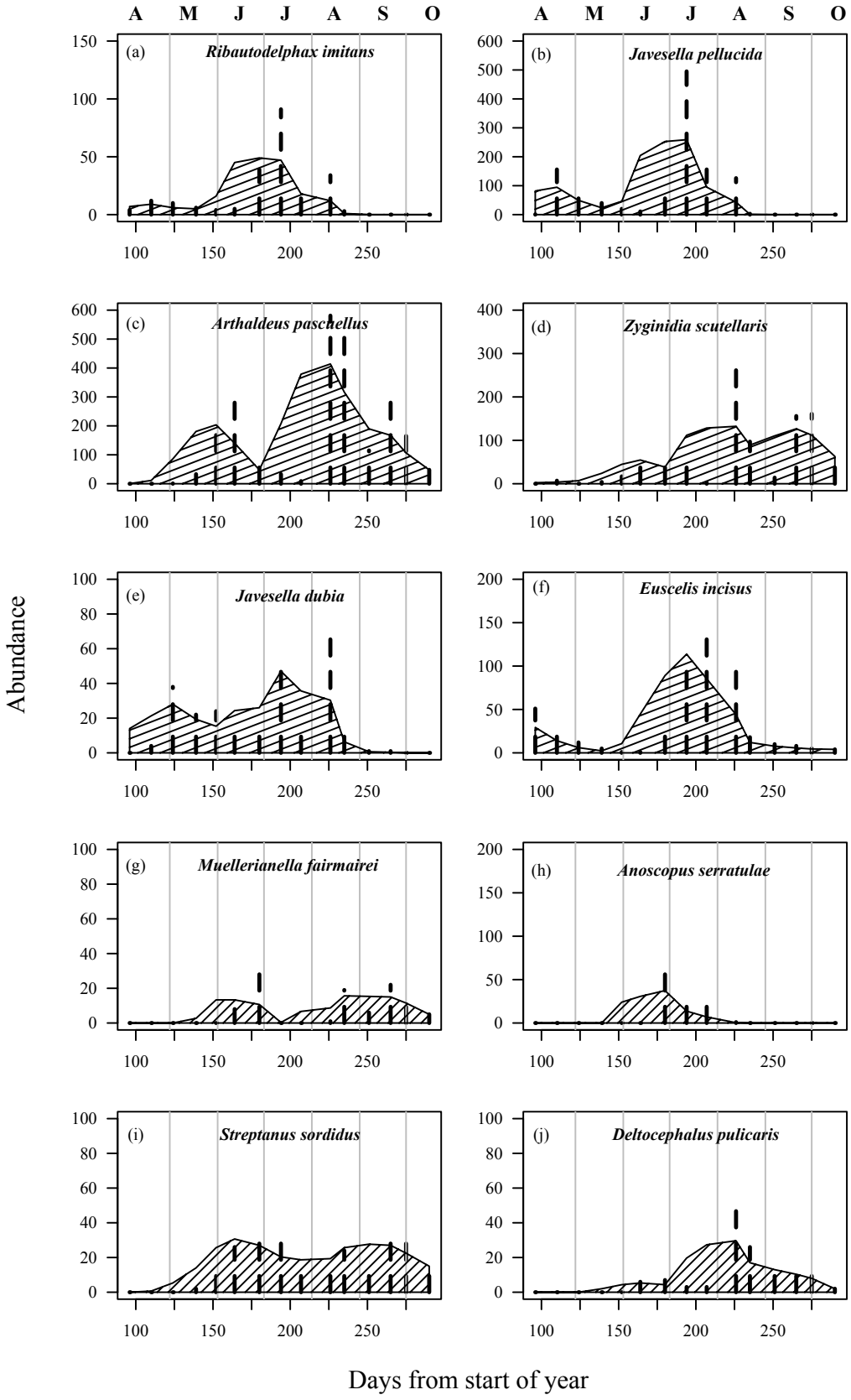

Fig. 4: Phenograms of the 10 commonest Auchenorrhyncha on Coe Fen. The vertical lines show raw abundance, and the shaded area the three date rolling average abundance.

environment is ecologically stable (Harrison et al. 2008) and species can be restricted because of their specificity or range limitations. Some species are highly specialised, requiring a subset of habitat characteristics in order to persist – for example these can be specific habitat gradients or host plants. Host plant drivers are unlikely to be the cause of *R. imitans* rarity, because of the geographically widespread host plant – tall fescue *Schedonorus* (*Festuca*) *arundinaceus* (Den Bieman 1987). Species can also be rare, because geographically they are at the edge of their range; where the environment is at the limit of their ecological tolerances (Goulson et al. 2005). The overlapping adult generations and community structure skewed in favour of *J. pellucida* could however suggest competitive interactions.

This study provided a unique look at how the life cycles of Auchenorrhyncha differentiate *R. imitans* from others in its community. It illustrated that there are considerable overlaps in adult generations in both the cicadellid and delphacid groups. Phenology can help mediate competition between species, however it can also aggravate competition (Dudley et al. 1990). Moreover, phenology can be altered by climate change; thus leading to the uncoupling of phenological relationships, and a trophic mismatch (Edwards & Richardson 2004). This is potentially more of an issue when one species is reliant upon the other; such as with pollinators and plants (Kudo & Ida 2013). Although understanding more about the interactions between those species that overlap – and those that do not – would enable a better understanding of how interactions drive the structure of similar grassland Auchenorrhyncha communities.

Detailed surveying of sites during delphacid peak abundance periods could help return more records for this species, certainly in the UK and potentially in the rest of Europe. Understanding more about the habitats and distributions of this species would enable a better understanding of rare species distributions in Auchenorrhyncha.

Zusammenfassung

Ribautodelphax imitans (Ribaut, 1953) (Hemiptera: Delphacidae) ist eine in ihrem gesamten Verbreitungsgebiet seltene Spornzikadenart, der in Großbritannien vorrangige Bedeutung im Naturschutz zukommt. Nach der Entdeckung eines Vorkommens der Art in Cambridge im Jahr 2010 wurde eine Studie zur Phänologie der Art und zu ihrer Einnischung in die lokale Zikadenartengemeinschaft durchgeführt. Dort ist die Art nicht selten, sondern eine der häufigsten Spornzikadenarten der Fläche, dominant ist allerdings *Javesella pellucida* (Fabricius, 1794). Der Grund für die Seltenheit von *R. imitans* auf nationaler Ebene bleibt unklar, möglicherweise sind starke interspezifische Interaktionen mit anderen zeitgleich auftretenden Arten ein wesentlicher Faktor.

Acknowledgements

This work represents part of a talk presented at the European Hemiptera Congress 2015, Austria. To attend, a grant was provided from the Royal Entomological Society. The authors would also like to thank Dr. Pete Brown from Anglia Ruskin University for helpful comments on the manuscript.

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